

Climate change and harmful benthic microalgae

Patricia A. Tester^{a,*}, R. Wayne Litaker^b, Elisa Berdalet^c

^a Ocean Tester, LLC, 295 Dills Point Road, Beaufort, NC, 28516, USA

^b National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC, 28516, USA

^c Institute of Marine Sciences (ICM-CSIC), Passeig Marítim de la Barceloneta, 37-49, 08003, Barcelona, Catalonia, Spain

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ABSTRACT

Sea surface temperatures in the world's oceans are projected to warm by 0.4–1.4 °C by mid twenty-first century causing many tropical and sub-tropical harmful dinoflagellate genera like *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* (benthic harmful algal bloom species, BHABs) to exhibit higher growth rates over much of their current geographic range, resulting in higher population densities. The primary exception to this trend will be in the tropics where temperatures exceed species-specific upper thermal tolerances (30–31 °C) beyond which growth slows significantly. As surface waters warm, migration to deeper habitats is expected to provide refuge. Range extensions of several degrees of latitude also are anticipated, but only where species-specific habitat requirements can be met (e.g., temperature, suitable substrate, low turbulence, light, salinity, pH). The current understanding of habitat requirements that determine species distributions are reviewed to provide fuller understanding of how individual species will respond to climate change from the present to 2055 while addressing the paucity of information on environmental factors controlling small-scale distribution in localized habitats. Based on the available information, we hypothesized how complex environmental interactions can influence abundance and potential range extensions of BHAB species in different biogeographic regions and identify sentinel sites appropriate for long-term monitoring programs to detect range extensions and reduce human health risks.

1. Introduction

Our planet is warming. An astounding eighteen of the nineteen warmest years have occurred in the twenty-first century; the past five years were the hottest since record keeping began (National Oceanic and Atmospheric Administration (NOAA), 2019). Temperature is a key factor in the growth, abundance and distribution of marine phytoplankton (Thomas et al., 2012; Wells et al., 2015; Gobler et al., 2017) and this portends significant health risks from harmful species as the oceans warm (Tester, 1996; Margalef, 1998; Moore et al., 2008; Hallegraef, 2010; Tester et al., 2010; Berdalet et al., 2015; Friedman et al., 2017). Phytoplankton species causing harmful blooms (HABs), while including fewer than five percent of known species (Sournia et al., 1991), have significantly negative consequences on human health, regional economies and food safety, especially in developing nations where seafood is a major source of protein (Food and Agriculture Organization (FAO) of the United Nations, 2016).

Monitoring programs for planktonic HAB species provide time-series data in some regions where HABs are endemic or recurrent, giving resource managers predictive capabilities regarding bloom

development, timing and effects of climate change on HAB distributions and abundances (Hallegraef, 2010; Wells et al., 2015; Gobler et al., 2017). In contrast, few long-term data sets are available for the subset of benthic microalgal species that cause harm (BHABs). BHABs are of unique concern because they disproportionately affect tropical regions where food security is an escalating problem with ocean warming (Tester, 1996). Climate change is expected to expand the geographic ranges of BHABs in the mid latitudes (Tester et al., 2013; Nishimura et al., 2013; Carnicer et al., 2016a; Farrell et al., 2016a; Rodríguez et al., 2017) and cause changes in seasonal patterns of occurrence (Tosteson, 2004; Nakada et al., 2018).

Benthic dinoflagellate species in the genera *Gambierdiscus* and *Fukuyoa* cause harm by producing neurotoxins (ciguatoxins and/or maitotoxins) that vector into marine food webs causing ciguatera fish poisoning (CFP) (Caillaud et al., 2010; Roué et al., 2016; Friedman et al., 2017; Darius et al., 2017, 2018a,b; Clausen et al., 2018; Hardison et al., 2018). Globally, CFP is the most common, non-bacterial illness associated with eating seafood, and while CFP is grossly underreported (90 %), there are ~50,000 cases documented annually, mostly from pantropical regions (Boucaud-Maitre et al., 2018). In the

* Corresponding author.

E-mail address: ocean.testler@gmail.com (P.A. Tester).

last decade seven new *Gambierdiscus* and one new *Fukuyoa* species have been described (Tester et al., 2019) and concomitantly CFP is being reported from places with no previous history of this illness (Pérez-Arellano et al., 2005; Caillaud et al., 2010; Farrell et al., 2016a).

From mid to late summer massive blooms of another BHAB genus, *Ostreopsis*, cause threats to human health in certain urbanized, temperate areas and are responsible for health concerns and beach closures. These events can result in lost revenue to tourist-dependent coastal communities (Lemée et al., 2012; International Conference on *Ostreopsis* Development (ICOD), 2012). Increasingly *Ostreopsis* blooms are recognized as the cause of mild respiratory illness and skin irritation throughout the Mediterranean and its adjacent seas (Gallitelli et al., 2005; Durando et al., 2007; Tichadou et al., 2010; Pfannkuchen et al., 2012; Vila et al., 2016, 2017). These health impacts have been attributed to the highly toxic, water-soluble, putative palytoxins (pPLTX) and their analogues (ovatoxins, OVTX) produced by *Ostreopsis*. Those impacts, however, have not been definitively proven. These toxins were rarely detected in the aerosol during blooms and, when present, do not correspond with human health symptoms (Ciminiello et al., 2014). Putative PLTX and OVTXs have been detected in some marine fauna in the Mediterranean Sea (Amzil et al., 2012) and *Ostreopsis*-related mass mortalities are reported for benthic marine organisms with limited mobility (starfish, sea urchins, crabs) (Vila et al., 2008; Totti et al., 2010). Fortunately, no associated seafood-borne illnesses have been documented from the Mediterranean coast by the European Centre for Disease Prevention and Control (ECDC) or the European Food Safety Agency (EFSA). In contrast, fatalities in tropical areas (Alcala et al., 1988; Randall, 2005; references in Lenoir et al., 2004) have been attributed to palytoxin-like compounds isolated from *O. siamensis*. In temperate waters of New Zealand, an *O. siamensis* bloom with some of the highest cell concentrations recorded worldwide (i.e. 1.4×10^6 cells g^{-1} macroalgae wet weight), was associated with a 40–60 % reduction in populations of the urchin, *Evechinus chloroticus*, a key herbivore in benthic communities (Shears and Ross, 2009). In Rhodes' (2011) review of the worldwide occurrence of *Ostreopsis*, she noted its distribution and associated illnesses had increased markedly in the last decade and predicted this trend would continue.

This review will focus on how habitats characterized by temperature, salinity, turbulence, light, pH, nutrients and substrates may change as oceans warm and how these changes affect distribution, abundance and human health risks associated with *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* species.

2. Expected climate changes by the mid-21st century

Temperature, salinity and pH are three environmental variables that affect growth and distribution of harmful benthic microalgae. The predicted changes in these factors by 2055 are detailed below.

2.1. Predicted temperature changes

Under an assumption that CO₂ emissions continue without significant abatement (RCP 8.5 in the 4th International Panel on Climate Change modeling convention), by 2055 sea surface water temperatures (SST) are projected to increase, on average, 0.4–1.4 °C in the Atlantic Ocean, 0.5–1.4 °C in the Pacific Ocean, 1.0–1.4 °C over most of the Indian Ocean; 1.0–1.4 °C in SST is predicted for the Caribbean Sea and Gulf of Mexico and 0.8–1.4 °C in the Mediterranean Sea (Fig. 1A, B; Meehl et al., 2007; IPCC, 2013; Brown et al., 2015; Nurse and Charlery, 2016). Representative, regional heating rates where BHABs occur are in the range of 0.37 to 0.45 °C decade⁻¹, in particular, 0.39 °C decade⁻¹ in Hawaii, 0.37 °C decade⁻¹ in the Gulf of Mexico, 0.37 °C decade⁻¹ along the southeast US coast, and 0.45 °C decade⁻¹ in the Mediterranean Sea (Alexander et al., 2018). This warming trend could be more pronounced during the summer months, particularly in more northerly latitudes, where greenhouse gas heating is integrated over a much shallower

mixed layer depth. As a result, the amplitude of seasonal SST cycles may increase as global temperatures increase (Alexander et al., 2018). While global climate model predictions vary, all forecast more frequent and intense temperature anomalies. Specifically, cold temperature extremes will decrease, and warm temperature extremes will increase relative to the historical period from 1956 to 2005.

2.2. Predicted salinity changes

Generally, in oceanic regions salinities average 30–40. Uncertainties about salinity changes at the local scale make it difficult to hypothesize how this key environmental parameter may affect HABs in the future (Wells et al., 2020). With warming of 1.5–2 °C climate models project heavy precipitation in some regions and the probability of precipitation deficits in others (Pachauri and Meyer, 2014). Models show a general decrease in salinity of 0.1–0.3 in the central and west central Pacific Ocean, the eastern and central Indian Ocean warm pool regions and the Baltic Sea by 2055 (Fig. 2A, B). Concurrently, increases of 0.2 in the Caribbean Sea and Gulf of Mexico and 0.2–0.3 in most of the temperate and tropical Atlantic Ocean are predicted (Fig. 2A, B). Increases in the Mediterranean Sea are expected to be more variable ranging from no change in the eastern basin to an increase of up to 0.4 in the western basin (Fig. 2A, B) (Durack and Wijffels, 2010; Skliris et al., 2014).

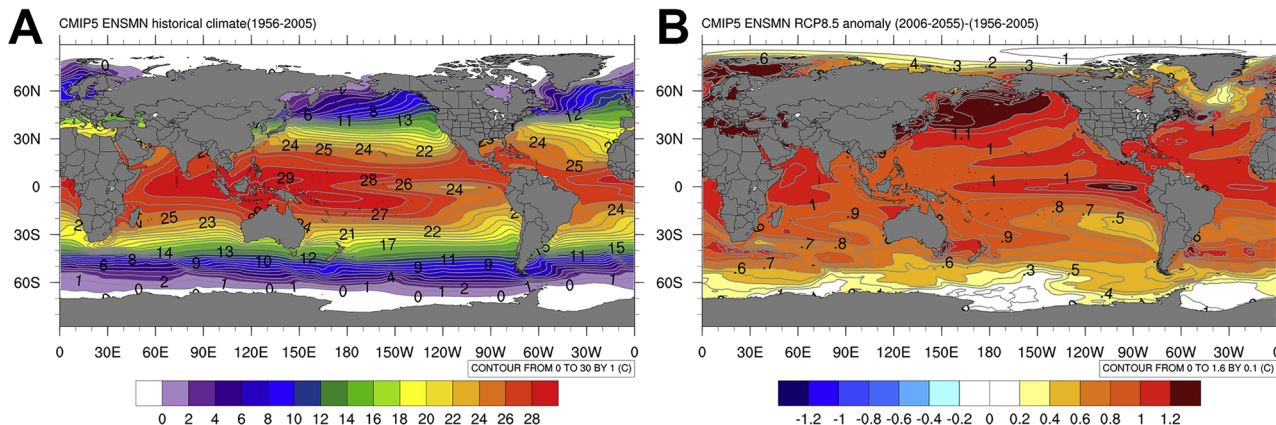
2.3. Predicted pH changes

Oceans have become 30 % more acidic over the last 150 years with strong latitudinal differences in temperature controlling the solubility of CO₂ in seawater. Ocean surface water pH currently ranges from approximately 8.04–8.20 (Fig. 3A, B). By 2055, pH decreases of 0.08–0.10 units are predicted in the central Atlantic and central Pacific Oceans, most of the Mediterranean Sea and Indian Ocean (Fig. 3B). More pronounced decreases of 0.10–0.12 units are expected in the temperate regions of the Atlantic and Pacific Oceans. As in the case of salinity, small scale changes in pH occurring in coastal regions will have direct effect on BHABs. In addition, the confounding effects of coastal eutrophication and associated increases in bacterial respiration need to be considered as well (Sunda and Cai, 2012). Model calculations show that acidification from respiratory CO₂ inputs interacts in complex ways with increasing atmospheric CO₂, resulting in a more than an additive decrease in pH at intermediate to higher water temperatures. Additional research on the physiological effects of pH on marine photo-synthetic organisms, in general, and of harmful species in particular, is needed (Wells et al., 2020).

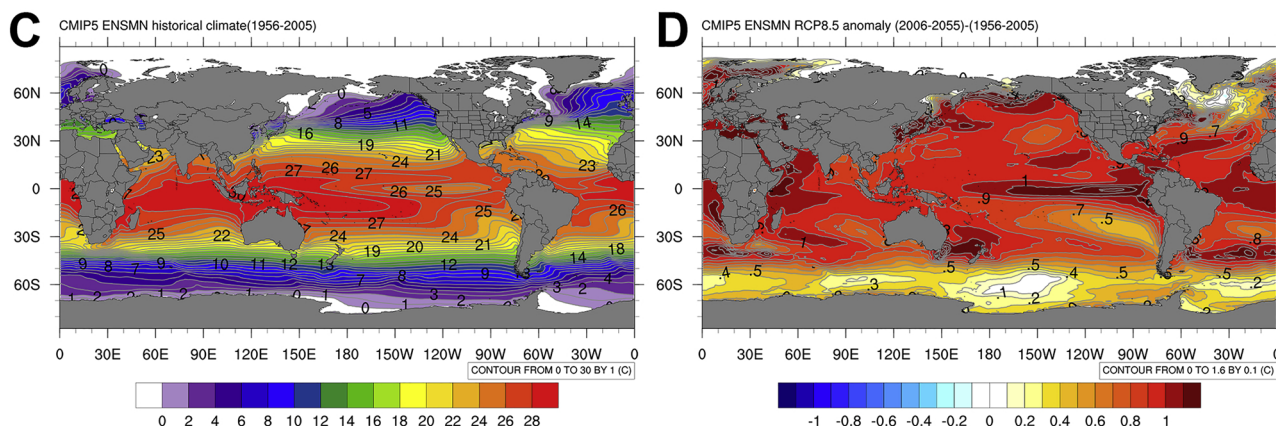
3. BHAB species, distribution, physiology, ecology, toxicity and habitat requirements: responses to environmental variables

Predicting how climate driven changes in temperature, salinity and pH, as well as other factors, will affect *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* species is impossible without prior knowledge of their diversity, distribution, physiology, toxicity and habitat requirements. Fortunately, research energized by a renewed interest in these species during the last decade has provided some valuable information. In this section we have summarized current information as a prerequisite for predicting how climate change is likely to affect *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* species. For *Gambierdiscus* and *Fukuyoa*, emphasis was placed on publications after 2009 following the revision of the genus *Gambierdiscus* and establishment of a definitive method for distinguishing species (Litaker et al., 2009; Vandersea et al., 2012; Fraga and Rodríguez, 2014; Fraga et al., 2016; Nishimura et al., 2016; Smith et al., 2016; Kretschmar et al., 2017; Rhodes et al., 2017a; Litaker et al., 2019). In the case of *Ostreopsis*, ribosomal RNA (rDNA) genes and internal transcribed spacer regions (ITS) has allowed the description of morphologically cryptic species and exploration of phylogenetic links, but much more work is still needed for this group (e.g., Leaw et al.,

Sea Surface Temperature ANN



Sea Surface Temperature JFM



Sea Surface Temperature JAS

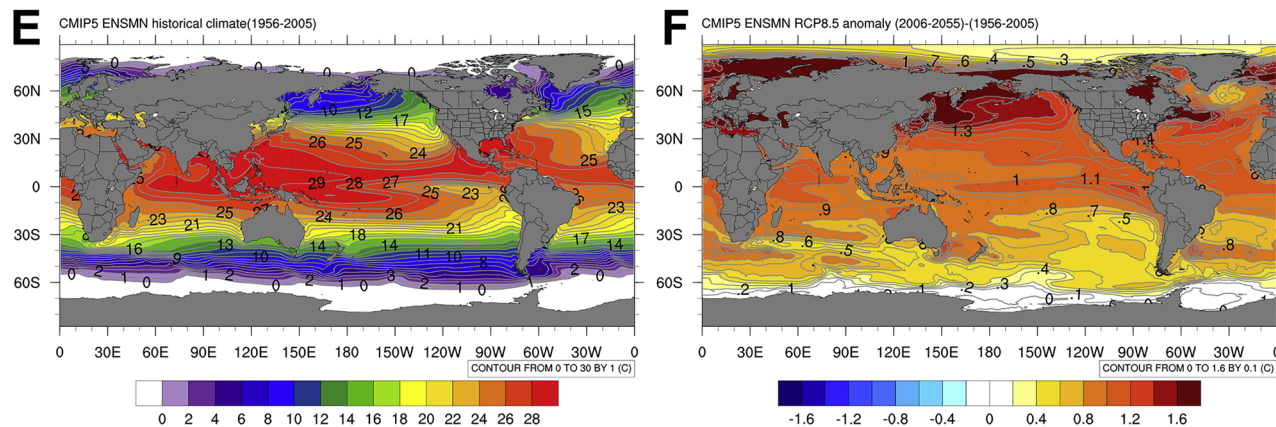


Fig. 1. Sea surface temperatures (SST, C°). A. Mean annual (ANN) temperatures over the historical period from 1956 to 2005. B. The average predicted increase in mean annual SST from 2006 to 2055. C. Mean January through March SST over the historical period from 1956 to 2005. D. The average predicted increase in mean January through March SST from 2006 to 2055. E. Same as C except for the July–September time period. F. Same as D except for the July–September time period. All these images were generated by averaging the results of 25 different climate models integrated into NOAA’s Climate Change Web Portal. This mapping tool was developed by the NOAA Earth System Research Laboratory, Physical Sciences and allows multiple model assumptions regarding future climatic conditions for numerous variables to be graphed and displayed (<https://www.esrl.noaa.gov/psd/ipcc/ocn/>).

2001; Penna et al., 2005, 2010, 2014; Sato et al., 2011; David et al., 2013; Hariganeya et al., 2013; Tawong et al., 2014).

3.1. *Gambierdiscus* and *Fukuyoa* distribution and toxicity

Historically, species in the genus *Gambierdiscus* Adachi & Fukuyo

were viewed as pantropical organisms distributed between 35°N and 34°S and ubiquitous throughout the Caribbean Sea, and the Pacific and Indian Oceans. Between 2016 and 2017 four new species were added to the genus *Gambierdiscus* from the south Pacific Ocean. In addition, four new species have been described in areas where *Gambierdiscus* was previously unknown, including two from the Canary Islands

Sea Surface Salinity ANN

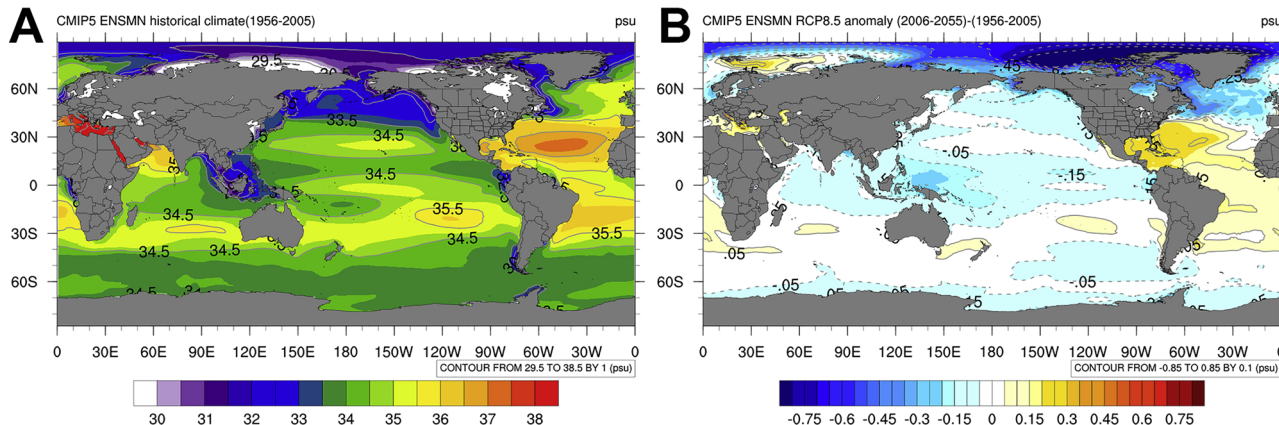


Fig. 2. Sea surface salinity. A. Mean annual salinity over the historical period from 1956 to 2005. B. The average predicted increase in sea surface salinity from 2006 to 2055. Figures were generated from NOAA’s Climate Change Web Portal as described in the legend of Fig. 1.

(Macaronesia), one from Japan and another from Korea. In total, there are now sixteen described *Gambierdiscus* species and three species of *Fukuyoa*, a closely related genus, previously included in the genus *Gambierdiscus* (Gómez et al., 2015). Among these nineteen species and five undescribed ribotypes (putative species), toxicity varies significantly (Table 1). Data on species occurrence, physiology and toxicity for *Gambierdiscus* and *Fukuyoa* from published literature have been augmented by distribution records from the Cawthron Institute Culture Collection, New Zealand, the Culture Collection of the Institut Louis Malardé, Tahiti and NOAA’s Beaufort Laboratory collection to produce a global distribution map (Fig. 4; Tester et al., 2019).

Gambierdiscus australes and two *Fukuyoa* species appear to have the widest latitudinal ranges from 40.00 °N to 35.25 °S (Table 1). It is important to note that without comprehensive sampling, occurrence records may not capture complete or even accurate information on the geographic ranges or patterns of species distributions. Newly described species will be underrepresented in current data bases (e.g., *G. lapillus*) as will species discovered during limited, regional studies (e.g. *G. scabrosus*). Other regions, especially the African coastal waters and the Indian Ocean, are under sampled so information is sparse. Once instituted, proposed BHAB monitoring programs may help fill these data gaps (Tester et al., 2018).

Research shows the majority of *Gambierdiscus* and *Fukuyoa* species analyzed to date produce only low levels of ciguatoxin (Table 1). One hypothesis is that low-toxicity species contribute only a small portion of

the toxin flux into the food chain compared to the highly toxic species (Litaker et al., 2017; Darius et al., 2017). In the Pacific Ocean, *G. polynesiensis* is understood to be the major ciguatoxin producer and has an impressive range extending 55.64 degrees of latitude between 24.78 °N and 30.86 °S (Fig. 4, Table 1). In Japanese waters, there is a possibility that *G. scabrosus* may contribute to local toxicity, but further documentation of the biogeography of this species, along with toxicity screening of additional isolates, are needed to confirm this possibility (Nishimura et al., 2016).

In the Caribbean Sea and Macaronesia (North Atlantic Ocean), *G. excentricus* is a species of concern. It is found as far north as 29.21 °N, in the Canary Islands, where it is associated with increasing CFP incidences involving as many as 100 victims (Pérez-Arellano et al., 2005; Boada et al., 2010; Otero et al., 2010; Bravo et al., 2015) who consumed locally sourced fish (Pérez-Arellano et al., 2005). The southernmost observation of *G. excentricus* is 22.74 °S, but this wide geographical range is somewhat misleading. This species is not abundant in tropical waters as might be surmised by its lower optimum growth temperature (Table 1). So, *G. excentricus* may only occur at higher latitudes or at depth in tropical or sub-tropical latitudes (Kibler et al., 2015; Litaker et al., 2019). Another species of concern in the Caribbean Sea and Atlantic Ocean is *G. silvae*. Currently this species is recorded only from Belize, Curaçao, Macaronesia and the US Virgin Islands (Fraga and Rodríguez, 2014; Litaker et al., 2009, 2019; Robertson et al., 2018), but with toxicity that rivals that of *G. polynesiensis* in the Pacific Ocean, it

pH at Surface ANN

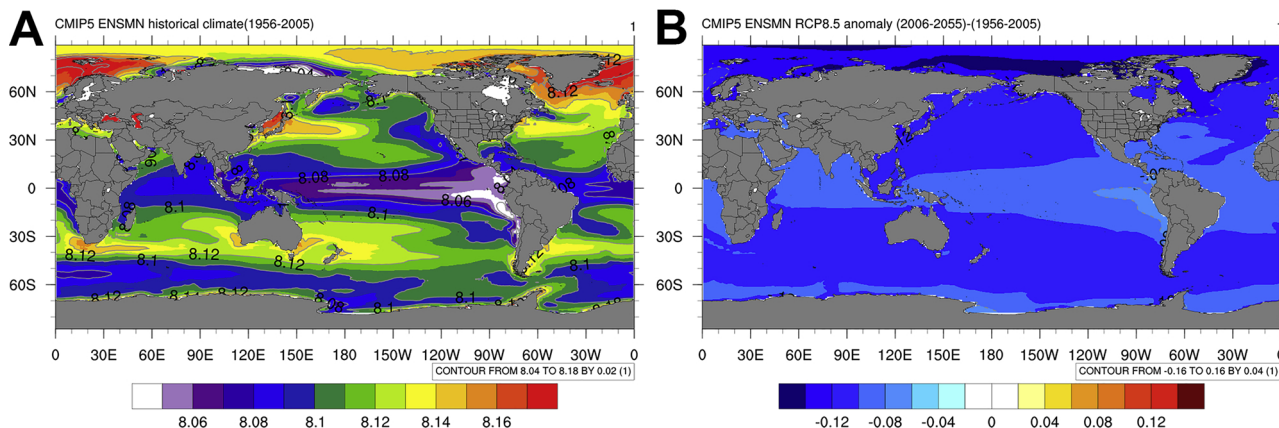


Fig. 3. Sea surface pH. A. Mean annual pH over the historical period from 1956 to 2005. B. The average predicted decrease in sea surface pH from 2006 to 2055. Figures were generated from NOAA’s Climate Change Web Portal as described in the legend of Fig. 1.

Table 1
 Summary of the *Gambierdiscus* and *Pukuyoa* literature regarding the taxonomic authority, type location, latitudinal distribution range, toxicity and known temperature, salinity and irradiance versus growth requirements for described and cryptic species (divergent clades in rDNA phylogenies).

Species Authority	Species Authority	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rates (°C)	Salinity Ranges for Positive, Optimum, and Maximum Growth Rates	Light Ranges for Positive and Maximal Growth Rates (μmol photons m ⁻² sec ⁻¹)
Type Location	Type Location					
Latitudinal Range in Decimal Degrees	Latitudinal Range in Decimal Degrees					
<i>Gambierdiscus australes</i> Chinain et al., 1999a	Austral Islands Archipelago, French Polynesia, south Pacific Ocean	MBA+; N2a+; 4 x 10 ⁻⁴ MU ND-22 fg PCTX3C eq. RBA ND fg total CTXs-LC-MS 640 x 10 ⁻⁴ MU 1,000 cells ⁻¹ MBA 0.6-2.7 fg CTX3C eq. N2a < 2.8-697 fg CTX1B eq. N2a	Chinain et al., 1999a Chinain et al., 1999a Chinain et al., 2010 Munday et al., 2017 Nishimura et al., 2013 Pisapia et al., 2017 Reverté et al., 2018	17.5 – > 30 19–28 25 Yoshimatsu et al., 2014	15.0 – > 41 20.4–38.6 32.1 Kibler et al., 2012	24–108 49 Kibler et al., 2012
40.00 N and 30.23 S				25 – > 40 27–38 30–35 Yoshimatsu et al., 2016		91–422 208 Yoshimatsu et al., 2016
<i>Gambierdiscus batechii</i> Fraga et al., 2016 (= <i>Gambierdiscus</i> sp. type 6; Xu et al., 2014; Dia et al., 2017)		MBA+; 3.4 fg CTX3C eq. N2a ND-19.9 fg PCTX1 eq. N2a	Fraga et al., 2016 Pisapia et al., 2017 Dia et al., 2017	–	–	–
Celebes Sea, Pacific Ocean						
2.52 N and 1.48 S						
<i>Gambierdiscus belizeanus</i> Litaker et al., 2009	Belize, Central America, Caribbean Sea	120 fg PCTX3C eq. RBA 0.43-2.49 fg CTX3C eq. N2a	Chinain et al., 2010 Litaker et al., 2017	20.0–35.0 24.5–31.7 28.2 Kibler et al., 2015	18.3 – > 41 22.4 – 36.7 28.4 Kibler et al., 2012	40 – 216 89 Kibler et al., 2012
29.43 N and 2.0 S				16.8–35.2 23.1–32.3 26.1–29.1 Xu et al., 2016	14.8–57.0 23.0–42.8 30.3–36.6 Xu et al., 2016	55 – > 400 100 – > 400 Xu et al., 2016
<i>Gambierdiscus caribbaeus</i> Litaker et al., 2009	Belize, Central America, Caribbean Sea	0.19-1.29 fg CTX3C eq. N2a 0.66 fg CTX3C eq. N2a	Litaker et al., 2017 Pisapia et al., 2017	16.5–35.0 24.5–31.9 28.6 Kibler et al., 2015	14.5 – > 41 20.9–39.4 35.0 Kibler et al., 2012	46–243 101 Kibler et al., 2012
27.87 N and 23.12 S				15.9–35.4 20.1–31.8 26.9–28.1 Xu et al., 2016	20–40 25–37 35 Tawong et al., 2016	< 55 – > 400 200 – > 400 Xu et al., 2016
				20.0–35.0 25–31 29 Tawong et al., 2016	10.4–55.1 22.5–44.0 30.1–34.4 Xu et al., 2016	40 – > 300 70 – > 300 160 Vacarizas et al., 2018
				19–33 25–31.0 29 Vacarizas et al., 2018	26–41 35–38 35 Vacarizas et al., 2018	

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Table 1 (continued)

Species Species Authority	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rates (°C)	Salinity Ranges for Positive, Optimum, and Maximum Growth Rates	Light Ranges for Positive and Maximal Growth Rates (μmol photons m ⁻² sec ⁻¹)	References
Gambierdiscus carolinianus Litaker et al., 2009	ND-1.03 fg CTX3C eq. N2a 3.3 fg CTX3C eq. N2a	Litaker et al., 2017 Pisapia et al., 2017	15.8–32.5 23.5–30.0 27.1 Kibler et al., 2015	20.9 – > 41 25.7–36.0 30.3 Kibler et al., 2012	58–115 88 Kibler et al., 2012	
North Carolina, Western Atlantic Ocean 35.33 N and 12.57 N			18.4–31.6 20.8–29.4 23.8–27.0 Xu et al., 2016	20.6–54.3 30.8–45.8 37.2–38.5 Xu et al., 2016	55 – > 400 100 Xu et al., 2016 < 20 – > 150 80–150 Leynse et al., 2017	
Gambierdiscus carpenteri Litaker et al., 2009	ND fg CTC3C eq. N2a 0.29–1.37 fg CTX3C eq. N2a ND fg total CTXs LC-MS 1.4 fg CTX3C eq. N2a	Darius et al., 2018a Litaker et al., 2017 Munday et al., 2017 Pisapia et al., 2017	17.5–35.0 22.7–32.3 29.2 Xu et al., 2016	< 14 – > 41 19.6–39.1 27.3 Kibler et al., 2012	55–388 151 Kibler et al., 2012	
Belize, Central America, Caribbean Sea 27.88 N and 36.88 S			16 – > 28 < 24 – > 28 – Sparrow et al., 2017	13.6–54.8 27.0–44.5 36 Xu et al., 2016	55 – > 400 200 – > 400 Xu et al., 2016	
Gambierdiscus cheloniae Smith et al., 2016	MBA + MTX-3+ by LCMS ND fg total CTXs LC-MS	Smith et al., 2016 Munday et al., 2017	– – – Sparrow et al., 2017	– – – Sparrow et al., 2017	– – – –	
Cook Islands south Pacific Ocean 21.23 N and 21.23 S						
Gambierdiscus excentricus Fraga et al., 2011	MTX-4+ 370-1,100 fg CTX1B eq. N2a 469 fg CTX1B eq. N2a 1,426 fg CTX3C eq. N2a	Fraga et al., 2011 Fraga et al., 2011 Litaker et al., 2017 Pisapia et al., 2017	20 °C 0.030 d ⁻¹ 24 °C 0.086 d ⁻¹ 27 °C 0.067 d ⁻¹ Unpublished data	– – – –	– – – –	
Canary Island, Macaronesia, northeastern Atlantic Ocean 29.12 N and 22.7361 S						
Gambierdiscus honu Rhodes et al., 2017b	MBA + MTX-3+ by LCMS; ND fg total CTXs LC-MS	Rhodes et al., 2017b Rhodes et al., 2017b Munday et al., 2017	– – – –	– – – –	– – – –	
Cook and Kermadec Islands, south Pacific Ocean 21.12 S and 29.27 S						

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Table 1 (continued)

Species Authority Type Location Latitudinal Range in Decimal Degrees	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rates (°C)	Salinity Ranges for Positive, Optimum, and Maximum Growth Rates	Light Ranges for Positive and Maximal Growth Rates (μmol photons m ⁻² sec ⁻¹)	References
Gambierdiscus jejuensis Nishimura et al., 2013 (= <i>Gambierdiscus</i> sp. type 2)	ND MBA	Nishimura et al., 2013	17.5 – > 30 21–28	< 20 – > 40 22–37	75–430 192	Yoshimatsu et al., 2016
Jeju Island, Korea, East China Sea 34.11 N and 26.13 N			Yoshimatsu et al., 2014 17 – > 30	Yoshimatsu et al., 2014 25–35		
Gambierdiscus lapillus Kretzschmar et al., 2017	MBA +, CTXs? by LC-MS CTX positive in FLIPR bioassay	Kretzschmar et al., 2017 Larsson et al., 2018b	–	–	–	–
Great Barrier Reef, Australia, Pacific Ocean 23.44 S and 21.25 S						
Gambierdiscus pacificus Chinain et al., 1999a	MBA +, N2a + 9 x 10 ⁻⁴ MU MBA ND fg PCTX3C eq. RBA 12.1–13.5 fg CTX3C eq. N2a 0.54–1.1 fg CTX3C eq. N2a 31.7–75.8 fg CTX1B eq. N2a ND fg total CTXs LC-MS	Chinain et al., 1999a Chinain et al., 2010 Pisapia et al., 2017 Darius et al., 2018a Caillaud et al., 2011 Munday et al., 2017	19.6–32.6 23.2–30.2 26.9 Kibler et al., 2012	< 18 – > 41 23.7 – > 41 29.9 Kibler et al., 2012	108–205 156 Kibler et al., 2012	
Tuamotu Archipelago, French Polynesia, Pacific Ocean 2.02 N and 23.12 S			18.8–34.5 22.4–32.8 26.2–28.7 Xu et al., 2016	15.5–53.8 28.8–42.3 35.6–36.9 Xu et al., 2016	< 55 – > 400 200–400 Xu et al., 2016	
Gambierdiscus polyestensis Chinain et al., 1999a	MBA +, N2a + 800–1500 x 10 ⁻⁴ MU MBA 17–4,400 fg PCTX3C eq. RBA 1,610–2,130 fg CTX3C eq. N2a 440 fg total CTXs LC-MS 18,200 fg CTX eq. LC-MS	Chinain et al., 1999a Chinain et al., 2010 Darius et al., 2018a Munday et al., 2017 Rhodes et al., 2014	–	–	–	–
Austral Islands and Tuamotu Archipelagos, French Polynesia, Pacific Ocean 24.78 N and 30.86 S						
Gambierdiscus scabrosus (= <i>Gambierdiscus</i> sp. type 1) Nishimura et al., 2016	MBA +, CTX + MBA 20 x 10 ⁻⁴ MU 1,000 cells ⁻¹ MBA 27.9 CTX3C eq. N2a	Nishimura et al., 2016 Nishimura et al., 2013 Pisapia et al., 2017	17.0 – > 30 25–30 30 Yoshimatsu et al., 2014	< 20 – > 40 24–36 30 Yoshimatsu et al., 2014	120–421 252 Yoshimatsu et al., 2016	
Kashiwa-jima Island off southern Honshu Japan 24.44 N and 34.77 N						
Gambierdiscus sibvae (= <i>Gambierdiscus</i> ribotype 1; Litaker et al., 2009) Praga and Rodriguez, 2014	19.6 fg CTX3C eq. N2a 10.3–12.4 CTX3C eq. N2a 2,100–4,800 fg C-CTX-1 eq. N2a	Litaker et al., 2017 Pisapia et al., 2018 Robertson et al., 2018	8.4–29.8 22.2–27.1 24.8 Xu et al., 2016	26.1–50.4 32.8–43.7 38.3 Xu et al., 2016	< 55 – > 400 100 Xu et al., 2016 < 30 – > 150 80–150 Leynse et al., 2017	
Canary Island, Macaronesia, northeastern Atlantic Ocean 12.12 N and 28.15 N						

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Table 1 (continued)

Species Authority	Type Location	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rates (°C)	Salinity Ranges for Positive, Optimum, and Maximum Growth Rates	Light Ranges for Positive and Maximal Growth Rates (μmol photons m ⁻² sec ⁻¹)	References
<i>Gambierdiscus toxicus</i> Adachi and Fukuyo, 1979; Litaker et al., 2009	Gambier Islands, French Polynesia, eastern Pacific Ocean 24.80 N and 23.14 S	ND MBA ND-28 fg PCTX3C eq. RBA	Adachi and Fukuyo, 1979 Chimain et al., 2010	-	-	-	-
<i>Gambierdiscus ribotype 2</i> Litaker et al., 2009	Belize, Central America, Caribbean Sea 27.88 N and 14.60 N	4.7–10.9 fg CTX3C eq. N2A	Litaker et al., 2017	19.8–33.0 24.5–30.1 27.4 Kibler et al., 2015	17.8–39.4 24.7–35.1 30.5 Kibler et al., 2012	43–185 89 Kibler et al., 2012	
<i>Gambierdiscus sp. type 3</i> Nishimura et al., 2013	Japan, Pacific Ocean 33.25 N	ND 10 ⁻⁴ MU 1,000 cells ⁻¹ MBA	Nishimura et al., 2013	15–25 22–25 25 Yoshimatsu et al., 2014	25 – > 40 29–37 35 Yoshimatsu et al., 2014	73–427 ≥427 Yoshimatsu et al., 2016	
<i>Gambierdiscus sp. type 4</i> Xu et al., 2016	Marakei, Republic of Kiribati, Pacific Ocean 2.00 N	2.6–6.0 fg P-CTX-1 eq. cell ⁻¹ N2a	Xu et al., 2016	17.6–31.1 22.8–28.1 25.6–25.7 Xu et al., 2016	25.1–54.1 32.0–44.7 36.4–38.1 Xu et al., 2016	< 55 – > 400 100 Xu et al., 2016	
<i>Gambierdiscus sp. type 5</i> Xu et al., 2016	Marakei, Republic of Kiribati, Pacific Ocean 2.00 N	0.01 fg P-CTX-1 eq. cell ⁻¹ N2a	Xu et al., 2016	20.1–31.9 22.0–30.1 27.9 Xu et al., 2016	20.0–50.1 26.6–40.1 32.9 Xu et al., 2016	< 55 – > 400 100–400 Xu et al., 2016	
<i>Fukuyoa paulensis</i> Gómez et al., 2015	Ubatuba, São Paulo, Brazil, south Atlantic Ocean 38.73 N and 35.25 S	MTX+, CTX- N2a 54-deoxy CTX1B + LC-MS ND fg total CTXs LC-MS	Gómez et al., 2015 Laza-Wartínez et al., 2016 Munday et al., 2017	-	-	-	
<i>Fukuyoa ruetzleri</i> Litaker et al., 2009; Gómez et al., 2015	Belize, Central America, Caribbean Sea 33.64 N and 16.80 N	MTX-3 0.88-24.5 fg CTX3C eq. N2a	Gómez et al., 2015 Litaker et al., 2017	16.8–35.1 24.5–31.9 28.5 Kibler et al., 2012	15.9 – > 41 19.6 – 35.7 24.7 Kibler et al., 2012	70 – > 700 231 Kibler et al., 2012	

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Table 1 (continued)

Species Authority	Type Location Latitudinal Range in Decimal Degrees	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rates (°C)	Salinity Ranges for Positive, Optimum, and Maximum Growth Rates	Light Ranges for Positive and Maximal Growth Rates (μmol photons m ⁻² sec ⁻¹)	References
<i>Fukuyoa yasumotoi</i> Holmes 1998; Gómez et al., 2015	Singapore Island, Pacific Ocean 40.00 N and 35.15 S	Unknown	-	-	-	-	-
<i>Fukuyoa ribotype HK Type 1</i> Leung et al., 2018	Hong Kong, China, Pacific Ocean 22.375 N	Extracts toxic to brine shrimp larvae	Leung et al., 2018	-	-	-	-

Optimum growth rate is defined as > 80 of the maximal growth rate observed. Abbreviations: Equivalents (eq.); Hemolytic Assay – ability of cellular extract to induce erythrocyte lysis versus a saponin control (HA); Mass Spectrometry (MS); Mouse Bioassay – toxicity determined by intraperitoneal injection of *Gambierdiscus* and *Fukuyoa* cellular extracts (MBA); Mouse Units, the 24 h LD₅₀ dose estimated using ~ 20 g mice (MU); Not Detectable = below detection limits (ND); neuroblastoma cell line cytotoxicity assay.

could be responsible for significant CFP risk depending on its abundance (Robertson et al., 2018).

Gambierdiscus australes is a global species of interest. Toxicity estimates for this taxon range from very low to relatively high indicating further research is requisite to determine if there are regional differences in ciguatoxin production (Table 1; Table S1 in Litaker et al., 2017; Pisapia et al., 2017; Reverté et al., 2018). With frequent occurrences across a wide latitudinal range, in all areas except the Caribbean Sea, the overall contribution of *G. australes* to toxin flux may be significant and marks it for consideration (Fig. 4).

3.2. *Ostreopsis* distribution and toxicity

The genus *Ostreopsis* Schmidt and type species *O. siamensis* Schmidt were first described from the Gulf of Siam (Thailand) in 1901. Serious attention was given to this taxon in the early 1980s due to its potential link with severe human poisonings in the region (Alcala et al., 1988) and subsequent identification of toxic *O. siamensis* and *O. mascarenensis* strains. Since then, the genus has been reported in other areas from tropical to temperate latitudes, with many records from Mediterranean beaches (Rhodes, 2011; Ciminiello et al., 2014; Table 2 and Fig. 5). There are now 11 recognized *Ostreopsis* species including two newly described ones, *O. fattorussoi* (Accoroni et al., 2016a) and *O. rhodesae* (Verma et al., 2016a) (Table 2). Identification of *Ostreopsis* species using light or scanning electron microscopy is difficult due to the morphological plasticity of key characters within and among species. Consequently, misidentification of *Ostreopsis* species, including the most commonly reported ones, *O. ovata* and *O. siamensis*, is frequent. Phylogenetic analysis of various ribosomal genes sequences (rDNAs) have proven successful in distinguishing species genetically (Penna et al., 2005; Sato et al., 2011; Penna et al., 2014). These analyses further revealed numerous novel ribotypes likely representing cryptic species. The ITS-5.8S and LSU DNA phylogenies of putative “*O. cf. ovata*” isolates collected over a broad geographic range indicate the *Ostreopsis ovata* complex is comprised of three distinct phylogenetic clades (Penna et al., 2014). Also, analysis of D1-D2 and D8-D10 large subunit rDNA genes has identified novel *Ostreopsis* ribotypes (*Ostreopsis* clades 1–7) from Japan and Thailand in the western Pacific (Sato et al., 2011; Tawong et al., 2014).

Assigning toxicity to certain *Ostreopsis* species is complicated because rDNA phylogenies indicate the original species descriptions encompass two or more cryptic species that have not yet been resolved taxonomically. To account for these taxonomic ambiguities, the current review listed the toxicity estimates from genetically identified isolates separately from those identified by morphology alone (Table 2). The following is a brief summary of the more extensive species-specific information listed in Table 2. For most of the species toxicity assessments are limited and these include *O. marinus* and *Ostreopsis* sp. 2, which appear non-toxic; *O. fattorussoi*, *O. heptagona*, *O. labens*, *O. mascarenensis* and *O. rhodesae* that appear toxic to varying degrees, and *Ostreopsis* sp. 7 which appears to be highly toxic. *Ostreopsis lenticularis* is comprised of two cryptic species, *Ostreopsis* sp. 5 and *Ostreopsis* sp. 6. The former is non-toxic to weakly toxic while the latter is highly toxic. *Ostreopsis cf. ovata* similarly includes three or more cryptic species. One of these, *O. cf. ovata* “Clade A” is well defined with numerous genetically identified isolates ranging in toxicity from non-toxic to highly toxic. The remaining *O. cf. ovata* cryptic species, including *Ostreopsis* sp. 1, may also demonstrate a similar range in toxicity, but this has yet to be systematically tested. We do know many *O. cf. ovata* complex isolates from the Mediterranean and Brazilian coasts exhibit high intracellular concentrations of diverse ovatoxins (OVTX-a to k), ostreocines (OSTR) and putative palytoxin analogues compared to the strains isolated off Ecuador and Thailand which appear non-toxic. *Ostreopsis siamensis* / *O. cf. siamensis* have been more thoroughly tested and appear to be only moderately toxic to non-toxic, with the non-toxic strains found in the Mediterranean Sea and moderately toxic ones in the Pacific Ocean. The

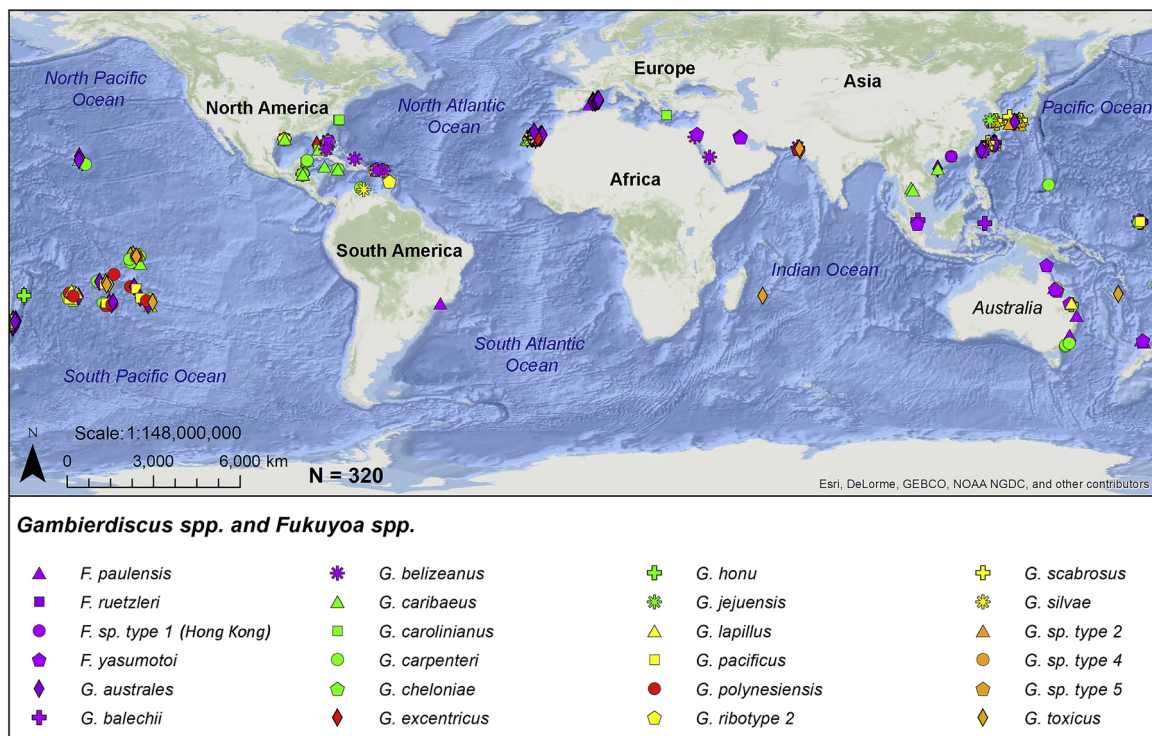


Fig. 4. Global occurrence of *Gambierdiscus* and *Fukuyoa* species from published records from 2009 to 2018. Duplicate reports from the same locality were omitted (after Tester et al., 2019).

toxicity of *O. belizeanus*, *O. caribbeanus*, *Ostreopsis* sp. 3, and *Ostreopsis* sp. 4 are currently unknown.

In general, the primary, known threat to human health, *Ostreopsis* pPLTX analogs, is low. They account for less than 1 % of the total toxin content in cells. When present, OVTX-a and b are usually the most abundant toxins, but some *Ostreopsis* isolates from the Mediterranean Sea have toxin profiles dominated by OVTX-b and f (Tartaglione et al., 2017). These findings suggest seafood-poisoning risks due to pPLTX, as reported in the tropics are low, but many uncertainties remain concerning the health impacts of OVTXs and OSTRs.

Currently, the main challenge of toxin analysis is identifying and quantifying the numerous, high molecular weight pPLTX analogues. It should be noted that *Ostreopsis* related toxins are considered as PLTX analogues, including OVTX, OSTR and putative PLTX (pPLTX). García-Altares et al. (2015) described the isobaric PLTX (iPLTX) as the pPLTX detected in other studies and recommended the use of the term isobaric PLTX in further studies. In this revision we have used the terms pPLTX and isobaric PLTX as synonyms, but we cite the toxins as indicated in the original references. Another impediment is the lack of OVTX, OSTR and PLTX standards derived from *Ostreopsis* species. The only available PLTX standards are those isolated from coral (*Palythoa*).

Toxicity of *Ostreopsis* species varies with the physiological status of the cells, nutrient availability and temperature (as shown in laboratory studies, e.g. Pistocchi et al., 2011; Scalco et al., 2012). The available data indicated most toxin production occurs during stationary phase growth in culture. Interestingly, experiments by Tosteson et al. (1989) showed that bacteria associated with the surfaces or the extracellular matrices of *O. lenticularis* were correlated with the development of peak dinoflagellate toxicity during the stationary phase of the cultures (Ashton et al., 2003). Additional well-controlled experiments with temperature adapted cultures are needed to determine how temperature affects *Ostreopsis* toxicity as a prerequisite for assessing human health risks in warmer oceans.

3.3. Effects of temperature on *Gambierdiscus* and *Fukuyoa* growth

In laboratory studies the lower thermal limit (LTL) for growth of *Gambierdiscus* and *Fukuyoa* species is between 15–20 °C (Table 1). Field populations, in temperate regions, however, are likely adapted to even lower temperatures with blooms of *G. carpenteri* reported at 16.5–17 °C in Merimbula, Australia where water temperatures can be as low as 8 °C (Kohli et al., 2014; Table 1C–F).

The upper thermal limit (UTL) for growth observed in laboratory studies is also species dependent and ranges from ~30 to 35 °C, with most species having a UTL < 33 °C (Table 1). The laboratory-based maximal growth temperatures (MGT) are known for *G. australes* (25 °C), *G. belizeanus* (26.1–29.1 °C), *G. caribaeus* (26.9–29.0 °C), *G. carolinianus* (23.8–27.1 °C), *G. carpenteri* (24–29.2 °C), *G. jejuensis* (25–26 °C), *G. pacificus* (26.2–28.7 °C), *G. scabrosus* (30 °C), *G. silvae* (24.8 °C), *Gambierdiscus* ribotype 2 (27.4 °C), *Gambierdiscus* sp. type 3, (25 °C), *Gambierdiscus* sp. type 4, (25.6–25.7 °C), *Gambierdiscus* sp. type 5 (27.9 °C) and *Fukuyoa ruetzleri* (28.5 °C) (Table 1). Equivalent growth data are unavailable for *F. paulensis*, *F. yasumotoi*, *Fukuyoa* ribotype HK Type 1, *G. balechii*, *G. cheloniae*, *G. excentricus*, *G. honu*, *G. lapillus*, *G. polynesiensis* and *G. toxicus*. When multiple isolates were tested, the optimal growth temperature (OGT) spans 3–5 °C. The difference between the upper OGT and UTL is typically only ~2–3 °C indicating a steep decline in growth as temperatures exceed the upper OGT. Experimental thermal limits for *G. excentricus* and *G. polynesiensis*, two of the more toxic species, are not available and can only be inferred by examining summer and winter temperatures over the known ranges of these species (Fig. 1C–F).

These data are consistent with a poleward migration of *Gambierdiscus* and *Fukuyoa* species as water temperatures increase provided annual SSTs remain above the species-specific LTL. Species adapted to cooler temperatures will be on the forefront of range extensions both north and south. A general decline in species abundance is predicted in tropical regions where temperatures are stable year-round and regularly exceed 30 °C for much of the year.

Table 2
Survey of the *Ostreopsis* literature regarding the taxonomic authority, type location, latitudinal distribution range, toxicity and known temperature, toxicity and irradiance versus growth requirement for the various described and cryptic species (divergent clades in rDNA phylogenies).

Species Authority	Species	Toxicity Measured by MS (pg cell ⁻¹)	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (C)	Salinity Ranges for Positive, Optimum and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (C)	Light Range for Positive, Optimum and Maximal Growth Rate(s) (µW cm ⁻²)
Type Location		or by Functional Assay		Reference(s)		
Latitudinal Range in Decimal Degrees						
<i>O. belizeanus</i> Faust, 1999	Unknown					
Belize, Caribbean Sea						
18.29 N and 16.49 N						
<i>O. caribbeanus</i> Faust, 1999	Unknown					
La Parguera, Puerto Rico, Caribbean Sea						
18.29 S and 12.50 S						
<i>O. fattorussoi</i> Accoroni et al., 2016a	0.28–0.94 pg·cell ⁻¹ MS OVTX-a (predominant) OVTX-d and -e	Accoroni et al., 2016b Tartaglione et al., 2016	Present in field 18–31.4 Highest field abundances 27–29.7 Accoroni et al., 2016b	Present in field 29.1–39.12 No correlation with abundance over this range Accoroni et al., 2016b Açaf et al., 2016		
Lebanon, Mediterranean Sea						
34.25 N and 34.65 N						
<i>O. heptagona</i> Norris et al., 1985	Toxic MBA	Norris et al., 1985	16–31 24–27 25 Morton et al., 1992	23–43 32–35 33 Morton et al., 1992	1.5 – > 5.5 4.5 Morton et al., 1992	
Knight Key, Florida, Gulf of Mexico						
24.7 N and 19.07 N						
<i>O. labens</i> Faust and Morton, 1995	Toxic by LC ₅₀ <i>Artemia franciscana</i> assays	Mohammad-Noor et al., 2007				
Man of War Cay, Belize Caribbean Sea						
24.34 N and 16.76 N						
<i>O. lenticularis</i> Fukuyo, 1981	209–1,113 MU × 10 ⁻⁶ MBA (= low toxicity) 0.2–2.0 MU × 10 ⁻⁶ field collected cells by MBA	Ashton et al., 2003 Bagnis et al., 1985				
(Includes the cryptic species <i>Ostreopsis</i> sp. 5; see Chomérat et al., 2019)	0–182 MU × 10 ⁻⁶ MBA using field collected cells No pPLTX activity by HA using sheep erythrocytes Not toxic, ND N2a assay Interact with nicotinic cholinergic receptors and voltage-dependent sodium	Ballantine et al., 1988 Carnicer et al., 2015b* Chomérat et al., 2019* Mercado et al., 1995				
Gambier and Society Islands, French Polynesia; New Caledonia						
28 N and 35.67 S						

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Table 2 (continued)

Species Authority	Type Location Latitudinal Range in Decimal Degrees	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (°C)	Salinity Ranges for Positive, Optimum and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (°C)	Light Range for Positive, Optimum and Maximal Growth Rate(s) (µW cm ⁻²)	Reference(s)
<i>O. martinus</i> Faust, 1999	The Main Channel, Twin Cays, Belize, Caribbean Sea 17.56 N and 12.5 S	channels 49–5,785 MU × 10 ⁻⁶ MBA Non-toxic MBA Inhibits acetylcholine response in guinea pig ileum (Note: isolate may be <i>O.</i> <i>stamensis</i>)	Tosteson et al., 1989 Sato et al., 2011 Tindall et al., 1990	-	-	-	-
<i>O. mascalensis</i> Quod, 1994	Rodrigues and Reunion Islands, Indian Ocean 21.15 N and 19.43 S and throughout southeast Indian ocean; Turquet et al., 1998; Hansen et al., 2001	Mascarenotoxin-A and -B, detected MS Toxic MBA	Lenoir et al., 2004 Lenoir et al., 2004	-	-	-	-
<i>O. ovata</i> / <i>O. cf. ovata</i> (Atlantic/ Mediterranean /Pacific clade – Clade A) Fukuyo, 1981	Gambier and Society Islands of French Polynesia and New Caledonia 17.43 S and 22.84 S	OVTX-a 0.065–171 OVTX-b 23–205 OVTX-c 3–37 OVTX-d/e 3–80 pPLTX = ND-24.8 isobPLTX Total HA horse erythrocytes Toxic HA sheep erythrocytes. Toxic to <i>Artemia</i> sp. nauplii Toxic to <i>Daphnia labrax</i> Nontoxic to highly toxic MBA Toxic in HA using rabbit erythrocytes NT MBA	Ben-Gharbia et al., 2016 Guerrini et al., 2010* Nascimento et al., 2012a* Nascimento et al., 2012a* Pezzolesi et al., 2012* Sechet et al., 2012* Granelli et al., 2011* Pezzolesi et al., 2012* Nascimento et al., 2012a* Tawong et al., 2015* Pezzolesi et al., 2012* Tawong et al., 2014*	17–37 22–30 25 Tawong et al., 2015* Pezzolesi et al., 2012* 11.1– > 30 - 22.5–30 Field Abdenmadher et al., 2017*	< 20 – > 40 28–35 30 Tawong et al., 2015* Pezzolesi et al., 2012*	-	-

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Table 2 (continued)

Species Authority	Type Location Latitudinal Range in Decimal Degrees	Toxicity Measured by MS (pg cell ⁻¹) or by Functional Assay	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (°C)	Salinity Ranges for Positive, Optimum and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (°C)	Light Range for Positive, Optimum and Maximal Growth Rate(s) (µW cm ⁻²)	Reference(s)
Gulf of Thailand, Thailand (Faust and Gullede, 2002)	41.40 N and 34.88 S	devoid of any appreciable toxicity. Lacks OSTR or OVTX. Japanese Strains contained OSTR-b OSTR-d pPLTX ND-0.8 Total ND-16 Extracts neurotoxic by metabolic activity, membrane potential, and cytosolic calcium level assays No toxicity MBA pPLTX ≤0.3 pg eq. cell ⁻¹ determined by hemolysis neutralization assay Low toxicity MBA Toxic to <i>Artemia salina</i> Low toxicity <i>Halobios virginea</i> larvae Extracts toxic to fish gill cell line RTgill-W1	Verma et al., 2016b*	29 Morton et al., 1992 Rhodes et al., 2000	33 Morton et al., 1992 Rhodes et al., 2000	4 µW cm ⁻² Morton et al., 1992	
Ostreopsis sp. 1 (<i>O. cf ovata</i> ribotype, clade B) Sato et al., 2011, Efimova et al., 2014	Coastal waters of Japan 35.575 N and 27.575 N	Highly toxic MBA	Sato et al., 2011	15–30 22–25 24 Tanimoto et al., 2013	25–40 33–36 35 Tanimoto et al., 2013	–	
Ostreopsis sp. 2 Sato et al., 2011	Cook Islands 47 S	Unknown		–	–	–	
Ostreopsis sp. 3 and 4 Sato et al., 2011	Cook Islands and Australia 21.22 S and 32.25 S	Unknown		–	–	–	
Ostreopsis sp. 6 (an <i>O. lenticularis</i> ribotype) Sato et al., 2011	Gulf of Thailand, Pacific Ocean 26.5 N and 1.2 N	Highly toxic MBA	Sato et al., 2011* Tawong et al., 2014* Carnicer et al., 2015b	16–30 22–30 24–25 Tawong et al., 2015* Tanimoto et al., 2013	< 20 – > 40 27.5–34 34–34.5 Tawong et al., 2015* Tanimoto et al., 2013	–	

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Table 2 (continued)

Species Authority	Toxicity Measured by MS (pg cell ⁻¹)	References For Corresponding Toxicity Values Listed in the Column to the Left	Temperature Ranges for Positive, Optimum, and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (°C)	Salinity Ranges for Positive, Optimum and Maximum Growth Rate(s) in Culture or the Ranges Over Which a Species Was Observed in the Field (°C)	Light Range for Positive, Optimum and Maximal Growth Rate(s) (µW cm ⁻²)
Type Location	or by Functional Assay		Reference(s)	Reference(s)	Reference(s)
Latitudinal Range in Decimal Degrees					
<i>Ostreopsis</i> sp. 7 Tawong et al., 2014	Highly toxic MBA	Tawong et al., 2014*	20 – < 30 22–29 25	< 20 – > 40 27.5–36 35	-
Thailand, Andaman Sea, Indian Ocean			Tawong et al., 2015	Tawong et al., 2015	
9.25 N and 8.25 N					

Optimum growth rate is defined as > 80–90% maximal growth rate observed. * = Isolate(s) identified genetically providing unambiguous confirmation of species and ribotype designations. Abbreviations: Equivalents (eq.); Hemolytic Assay – ability of cellular extract to induce erythrocyte cell lysis versus a saponin control (HA); Ovatoxin (OVTX); Ostreocin (OSTR); Mass Spectrometry (MS); Mouse Bioassay – toxicity determined by intraperitoneal injection of *Ostreopsis* cellular extracts (MBA); Mouse Units, the 24 h LD₅₀ dose estimated using ~ 20 g mice (MU); Not Detectable = below detection limits (ND); neuroblastoma cell line cytotoxicity assay (N2a); putative palytoxin like toxin = isobaric PLTX (García-Altres et al., 2015) (pPLTX).

3.4. Effects of temperature on *Ostreopsis* growth

The variations in OGT for *Ostreopsis* species are similar to those observed for *Gambierdiscus* species and range from 22 to 30 °C (Morton et al., 1992; Nascimento and Corrêa, 2010; Granéli et al., 2011; Scalco et al., 2012; Vidyarthna and Granéli, 2012; Yamaguchi et al., 2012; Tanimoto et al., 2013; Coahu et al., 2013). Species-specific optima, where growth exceeds 80–90 % of the maximal rate are available for some *Ostreopsis* species (Table 2). These include *O. heptagona* (24–27 °C), *O. ovata* / *O. cf. ovata* Clade A (22.5–30 °C), *O. cf. ovata* isolates with unknown clade associations (22–30 °C), *O. siamensis* / *O. cf. siamensis* (28–31 °C), *Ostreopsis* sp. 6 (22–30 °C) and *Ostreopsis* sp. 7 (22–29 °C). The field data indicate that maximum abundances of *O. fattorussoi* occur between 27 and 29.7 °C, which may or may not indicate temperature growth optima.

Ostreopsis cells, in contrast to most *Gambierdiscus*, can tolerate temperatures between 7–13 °C (Coahu et al., 2013; Selina et al., 2014). In temperate latitudes, blooms typically occur between mid-summer to mid-fall when temperatures exceed 17–22 °C and are most frequent at 22–29 °C (Nascimento et al., 2012a,b; Mangialajo et al., 2011; Pistocchi et al., 2011; David et al., 2012b; Coahu et al., 2013; Selina et al., 2014; Accoroni et al., 2015; Accoroni and Totti, 2016). Currently, there are apparent inconsistencies in reports of temperatures and bloom development for the same *Ostreopsis* species (Accoroni and Totti, 2016), likely due to the misidentification of species with different temperature optima being identified as the same species (Pistocchi et al., 2011; Tawong et al., 2014). Additional *in situ* observations of blooms, in combination with definitive molecular identifications, will help clarify the role temperature plays in controlling species-specific *Ostreopsis* blooms. Finally, if threshold temperatures regulate cyst germination in *Ostreopsis*, this information will be critical in understanding bloom formation (Bravo et al., 2012; Accoroni et al., 2014; Selina et al., 2014; Accoroni and Totti, 2016; Verma et al., 2016b).

3.5. Effects of salinity on *Gambierdiscus*, *Fukuyoa* and *Ostreopsis*

The shallow ecosystems where BHABs occur may be highly influenced by coastal freshwater inputs and high variations in salinity. Early studies by Taylor (1985) noted *Gambierdiscus* was more prevalent and abundant around small, dry islands, reefs, or pinnacles with relatively high salinities. Subsequent laboratory studies show *Gambierdiscus* species are broadly euryhaline with > 80 % maximal growth rates occurring at salinities between ~20 to 44, with highest growth typically found around ~25–38 (Kibler et al., 2012; Xu et al., 2016; Table1). In most locations where *Gambierdiscus* grows, salinities remain sufficiently high that cell abundances are unaffected (Chinain et al., 1999b; Chateau-Degat et al., 2005; Parsons and Preskitt, 2007; Fig. 2A, B). In regions heavily impacted by seasonal rains or river discharges, with salinities often below 24–25, *Gambierdiscus* populations are reduced or excluded (Hokama et al., 1993; Delgado et al., 2006; Catania et al., 2017; Nishimura et al., 2018). *Gambierdiscus* also fails to flourish in nearshore waters receiving runoff from larger landmasses even when the ambient salinities remain relatively high (Yasumoto et al., 1980; Carlson and Tindall, 1985). The cause for this inhabitation is not known.

Overall the reported salinity growth optima for *Ostreopsis* species ranges from 30 to 40, with relatively high growth or abundances occurring at salinities as low as 25 and as high as 45 (Morton et al., 1992; Pistocchi et al., 2011; Yamaguchi et al., 2012; Tanimoto et al., 2013; Yoshimatsu et al., 2014; Carnicer et al., 2016b; Accoroni and Totti, 2016; Abdennadher et al., 2017; Boisnoir et al., 2018; Table 2). Influence of river plumes with salinities below 20 are not favorable to *Ostreopsis* blooms (Carnicer et al., 2015a). Establishing a direct relationship between salinity and *Ostreopsis* abundance in field studies is equivocal, ranging from an inverse relationship for *O. ovata* in Hawaii, to no relationship for *O. heptagona* from the Gulf of Mexico (Okolodkov

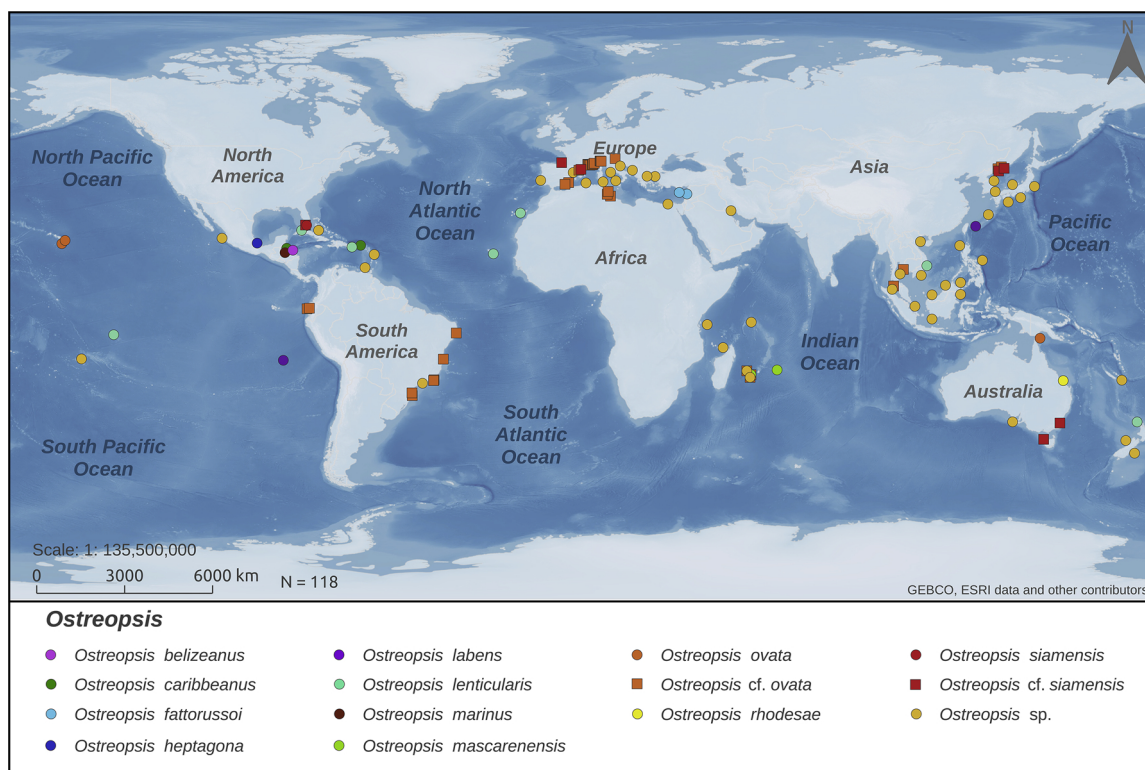


Fig. 5. Global occurrence of *Ostreopsis* species. Data are from published records 1995–2019, including those illustrated in *Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB)*, 2012 and Rhodes (2011). Duplicate reports from the same locality were omitted.

et al., 2007), to *Ostreopsis* blooms being favored by higher salinities in the Mediterranean Sea (Vila et al., 2001; Cohu et al., 2011; Pistocchi et al., 2011; Carnicer et al., 2016b). Likely, the response to salinity is affected by other local environmental parameters (nutrients, hydrodynamics) covarying with salinity. Given the small range of salinity variability expected from climate change, it could be hypothesized this environmental factor will not have a direct effect on BHABs dynamics.

3.6. Effects of depth and light on *Gambierdiscus*, *Fukuyoa* and *Ostreopsis*

A major unresolved issue for *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* species is their distribution with depth, which is co-dependent on light availability, suitable substrate and exposure to turbulence. Depth is also auto correlated with decreases in temperature, typically from 0 to $> 1.0^{\circ}\text{C}$ over 150 m (Kibler et al., 2015). Given that some *Gambierdiscus* species are more toxic than others, depth distribution could affect the source of ciguatoxins in the food webs because several of the more toxic species have lower thermal tolerances (Kibler et al., 2012; Litaker et al., 2017; Pisapia et al., 2017). Less is known about the distribution of *Ostreopsis* populations with depth and how this might affect their overall impacts on human and animal health.

The fourteen *Gambierdiscus* species examined to date in laboratory experiments maintain positive growth rates at irradiances as low as $6\text{--}17\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$, comparable to other dinoflagellates species (Kibler et al., 2012; Xu et al., 2016; Singh and Singh, 2015; Yoshimatsu et al., 2016; Leynse et al., 2017; Table 1). These irradiances occur at depths of 150 m in clear tropical waters (Kibler et al., 2012). *Gambierdiscus* have been found in samples collected between 0–45.7 m (Richlen and Lobel, 2011; Tester et al., 2013), with deeper depths not yet sampled. Maximal species-specific growth rates occur between $40\text{--}450\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$. Optimal species-specific growth rates ($> 80\%$ maximum) typically occurred between $\sim 25\text{--}150\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ similar to other dinoflagellates (Kibler et al., 2012; Yoshimatsu et al., 2016; Xu et al., 2016; Leynse et al., 2017; David

et al., 2018; Table 1). These irradiances are characteristic between $\sim 12\text{--}75\ \text{m}$ on sunny days. Sustained irradiances above $300\text{--}700\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ cause significant growth inhibition depending on the species. *Gambierdiscus* species are thought to manage exposure to inhibitory light levels encountered in the upper water column by utilizing macrophytes or other substrates for shade (Ballantine et al., 1988; Nakahara et al., 1996; Villareal and Morton, 2002). There is also evidence species photo adapt to withstand exposure to irradiances exceeding $250\ \mu\text{mol photons m}^{-2}$ for at least short periods (Leynse et al., 2017).

The field data on *Gambierdiscus* distribution with depth are contradictory. Some studies show increased abundances in the first few meters (Taylor, 1985; Boisson et al., 2018). Other studies document greater cell abundances between 10–40 m depth, where light is attenuated to $< 60\%$ of surface irradiance (Richlen and Lobel, 2011; de Sylva, 1982; Litaker et al., 2009; Yoshimatsu et al., 2016), or no difference between 1–20 m (Loeffler et al., 2015; Xu et al., 2016). These data suggest *Gambierdiscus* will not be light limited if they seek refuge at greater depths in regions where surface temperatures exceed $30\text{--}31^{\circ}\text{C}$ with climate change.

Data on the light requirements for *Ostreopsis* are limited. Cells grow optimally at $100\text{--}330\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ with $> 80\%$ maximal growth between $90\text{--}460\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ (Morton et al., 1992; Sechet et al., 2012; Yamaguchi et al., 2012). This optimum light intensity occurs in shallow intertidal regions to depths of 13–28 m in the Mediterranean Sea and Sea of Japan where toxic blooms are common (Mangialajo et al., 2011; Selina et al., 2014; Vila et al., 2016). *Ostreopsis ovata* was shown to grow well from 100 to $550\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$, but not at $10\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ (Monti and Cecchin, 2012). These data indicate *Ostreopsis* should grow well above 30–50 m and one study has shown they are present at depths of 30 m (Cohu and Lemée, 2012). Field studies report highest densities generally occur from the surface to 3 m and decline rapidly below that depth in less turbulent environments where blooms develop (Totti et al., 2010; Cohu et al., 2013; Boisson

et al., 2018). The main exception reported was for *Ostreopsis siamensis*, which was sampled at depths of 3, 5, 8 and 12 m at two sites (Mabrouk et al., 2011). In this study one site received more wave action than the other. *Ostreopsis* were more abundant in the deep station with lower light levels and more sheltered conditions than at inshore shallower stations, subjected to higher turbulence. Research is needed to establish whether high-density *Ostreopsis* populations exist at 10–30 m depth and, if not, what factors other than light might be limiting.

3.7. Effects of CO₂ on *Gambierdiscus*, *Fukuyoa* and *Ostreopsis*

Photosynthetic carbon fixation is accomplished by the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO), which has a low affinity for its inorganic carbon substrate, CO₂ (Reinfeldt, 2011). To overcome this CO₂ substrate limitation, marine phytoplankton have evolved carbon concentrating mechanisms (CCMs) to increase chloroplast CO₂ concentrations facilitating more efficient C-fixation by RubisCO. Dinoflagellates evolved over 500 million years ago when CO₂ levels were high, consequently they have a RubisCO variant with a relatively low affinity for CO₂ (Badger et al., 1998; Van de Waal et al., 2019). As CO₂ levels declined over time due to greater photosynthetic demand, dinoflagellates evolved moderately efficient CCMs. In the 21st century ocean pH is expected to decline between 0.14 and 0.35 units (IPCC, 2007; Fig. 3). This pH decline will elevate ambient CO₂ enhancing growth and promote higher primary productivity by as much as 40% (Schippers et al., 2004; Huang et al., 2018). The one field study specific to BHABs found no trends in the distribution of *Ostreopsis cf. ovata* populations growing along a pH gradient in volcanic CO₂ vents of the Ischia Island (Tyrrhenian Sea, Mediterranean Sea). Di Cioccio et al. (2014) concluded ocean acidification would not constrain the range or intensity of *Ostreopsis* blooms. A recently published meta-analysis indicates elevated pCO₂ and warming will work synergistically with increasing temperatures to promote algal growth and toxin production, supporting the proliferation and toxicity of HABs (Brandenburg et al., 2019).

3.8. Effects of turbulence on *Gambierdiscus*, *Fukuyoa* and *Ostreopsis*

Blooms of planktonic dinoflagellates are favored by low turbulence environments (Margalef, 1978), and *Gambierdiscus* and *Ostreopsis* species tend to reach highest abundances in relatively sheltered habitats protected from strong wave action and prevailing currents (e.g. Taylor, 1985; Shears and Ross, 2009; Totti et al., 2010; Nascimento et al., 2012a,b; Okolodkov et al., 2014; Anhalt et al., 2016; Loeffler et al., 2018). Species in both genera are adapted for increased survival in the benthic environments having evolved a flattened morphology and the ability to produce adherent mucus. Though each genus thrives in relatively low to moderate turbulence environments, within the same habitat, *Ostreopsis* is almost always more abundant than *Gambierdiscus* (Grzebyk et al., 1994; Kibler et al., 2012). This may be due to *Gambierdiscus* species having inherently slower growth rates on average (0.05–0.35 d⁻¹) compared to *Ostreopsis* species (0.17–0.5 d⁻¹) (Morton et al., 1992; Kibler et al., 2012; Scalco et al., 2012; Yamaguchi et al., 2012; Tanimoto et al., 2013; Xu et al., 2016). Slower growth would also make it more difficult to compensate for losses due to turbulent dispersion (Bomber, 1985; Grzebyk et al., 1994; Delgado et al., 2006; Yamaguchi et al., 2012).

Understanding the full impact of turbulence is hampered by a lack of concurrent quantitative measurements of turbulence kinetic energy dissipation rates (epsilon) in both *in situ* and experimental studies (Guadayol et al., 2009). Accurately measuring these dissipation rates in the small-scale environments where BHAB species live is extremely difficult. As a result, the precise levels of water motion that affect the competitiveness and successional patterns of BHAB species remains largely unknown. Despite the difficulties involved with quantifying turbulence, field observations leave little doubt that turbulence plays a

crucial role in *Ostreopsis* bloom dynamics. In Peter the Great Bay, Selina et al. (2014), found *Ostreopsis* spp. reached higher densities at sites with moderate turbulence compared to calm inner Bay locations or exposed sites with strong wave action.

Numerous studies have shown the dense mucous aggregates of *Ostreopsis* cells that form on macrophytes are released mainly due to wave action (Vila et al., 2001; Aligizaki and Nikolaidis, 2006; Mangialajo et al., 2008; Shears and Ross, 2009; Totti et al., 2010). Freed cells often remain suspended in the water column or float to the surface. The relationship with turbulence, however, is more complicated than fostering cell release. Laboratory experiments revealed that shaken *O. cf. ovata* populations entered stationary phase earlier, reached lower cell yield and had 30% lower OVTX-a intracellular content compared to control flasks maintained under still conditions (Vila et al., 2016). This suggests elevated turbulence could retard bloom development and simultaneously modulate toxin production. The level of turbulence required for cell release is also related to the mucus layer characteristics (thickness, chemical composition, adherence properties), which vary with the physiological state of the cells (Heil, 1993). The more adherent the cells are, the more resistant they are to resuspension. As the benthic blooms intensify, the protective mucus they produce also changes water viscosity at the cell surface. This affects nutrient and gas diffusion to and from the cell, and may contribute to cells becoming nutrient limited, and perhaps more susceptible to release by wave action. Finally, dispersal of sufficient biomass causes the bloom to collapse and may facilitate initiation of blooms in other locations (Jenkinson et al., 2014).

3.9. Effect of nutrients on *Gambierdiscus*, *Fukuyoa* and *Ostreopsis*

Gambierdiscus and *Fukuyoa* are often associated with benthic habitats where recycling is high and nutrients are readily available for uptake. It has been postulated that *Gambierdiscus* cells obtain nutrients directly from associated organisms such as algal turfs and macrophytes (Carlson, 1984; Carlson and Tindall, 1985). If true, cells are rarely nutrient limited. This may account for why ambient nutrient concentrations are not correlated with *Gambierdiscus* abundances. Direct experimental evidence for nutrient sufficiency comes from Loeffler et al. (2015), who found no *Gambierdiscus* growth enhancement in experimental field plots receiving supplemental nutrients.

The role of nutrients in regulating *Ostreopsis* blooms is not well established (Vila et al., 2001; Shears and Ross, 2009; Cohu et al., 2011; Pistocchi et al., 2011; Accoroni et al., 2015; Fricke et al., 2018). Various studies have indicated the availability of inorganic and organic nitrogen and phosphorus are important in promoting bloom development (Parsons and Preskitt, 2007; Cohu et al., 2013; Accoroni et al., 2015; Jauzein et al., 2017).

The extent to which nutrients may influence the distribution of *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* during climate change is uncertain. In the case of *Gambierdiscus*, increased runoff from land is likely to be more of an issue than overall nutrient concentrations in governing where optimal growth will occur in newly colonized habitats (see Section 2.2). The limited data available for *Ostreopsis* show that it tolerates or benefits from increased nutrient levels (Pistocchi et al., 2011 and references therein). Regions where climate change is expected to increase precipitation and associated nutrient inputs will likely experience more intense and prolonged *Ostreopsis* blooms.

3.10. Substrates

Substrates for *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* include macroalgae (Carlson, 1984; Grzebyk et al., 1994; Faust, 1995; Mohammad-Noor et al., 2007; Monti et al., 2007; Aligizaki and Nikolaidis, 2006; Catania et al., 2017), algal turfs and live corals (Grzebyk et al., 1994; Parsons and Preskitt, 2007; Yong et al., 2018), dead corals (Grzebyk et al., 1994) and sand (Faust, 1995). These organisms can also swim freely within the water column for short periods, become entangled in

detritus or other aggregates and live within interstitial spaces at the sediment water interface (Faust, 2009). Comparative surveys of macroalgal hosts or substrates were equivocal and revealed no consistent trends in overall substrate preference (Litaker et al., 2010; Sparrow et al., 2017; Nishimura et al., 2018). Cell abundances on different substrate types, too, are quite variable over time and space even in the same habitat (Yong et al., 2018).

Yong et al. (2018) undertook the first statistically robust study of how various substrate types (biological and non-biological) govern the abundance of *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* species. They used the artificial substrate method to obtain an integrated estimate of cell numbers at multiple sites on a Malaysian fringing reef system over the course of a year (Tan et al., 2013; Tester et al., 2014; Jauzein et al., 2016, 2018; Moreira and Tester, 2016; Mangialajo et al., 2017; Tester and Kibler, 2018). The substrates at each site were photographed and catalogued. Cluster analysis allowed classification of the sites into objectively quantified substrate types. *Gambierdiscus* were widely distributed throughout the range of microhabitats investigated and present in ~80 % of samples from habitats types with high coral cover and ~70 % from habitats dominated by sand or coral rubble. Interestingly, *Gambierdiscus* occurrence in microhabitats with high macroalgal cover was low (36 % of samples). No cells were detected in microhabitats with substrates primarily comprised green and brown macroalgae. The highest *Gambierdiscus* abundances were found in microhabitats dominated by algal turfs associated with coral rubble and were low elsewhere. The study further noted *Gambierdiscus* cells were rarely present in January when wet monsoon conditions prevailed. Cell abundances increased with onset of the dry monsoon and warmer temperatures, and then declined during the hottest part of the year when SSTs were highest (32 °C). Cell densities recovered, to some extent, as temperatures declined again, before the onset of the wet monsoon season. Additional detailed habitat studies of this type are needed to gain a better understanding of how local microhabitat differences govern the relative abundance of the various species.

In the tropics *Ostreopsis* can thrive in diverse microhabitats whose dominant substrate types include hard coral, coral rubble, red filamentous algae and sand (Faust, 1999; Okolodkov et al., 2007). Many studies from temperate environments alternatively report *Ostreopsis* prefer turf algae, macrophytes or hard substrates (Totti et al., 2010; Selina et al., 2014; Mangialajo et al., 2017), while still others report no specific substrate preference (Cohu et al., 2013). These observations indicate complex interactions between substrates and other factors govern where *Ostreopsis* species predominate. A recent study in the Mediterranean reported sites dominated by turf-forming species (*Ceramiales*) supported the highest total *O. cf. ovata*, while the lowest cell numbers were found in *Cystoseira* (foliose brown algae) dominated communities (Catania, 2017). In this case, the preponderance of turf forming algae were indicative of degraded habitats, while habitats dominated by *Cystoseira* represented healthier, more diverse benthic communities. These results are consistent with observations of high *O. cf. ovata* abundances at sites heavily impacted by human stressors where healthy macroalgal communities were replaced by more hard surfaces dominated by turf algae.

4. Regional examples

Using climate change projections in conjunction with regional scale meteorological forecasts (Hobday et al., 2018) permits closer examination of factors that may affect BHAB habitats, growth rates, cell abundances and range extensions, all of which are relative to changing human health risks. The examples selected below involve multiple environmental factors that illustrate how these factors may affect global *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* distribution and abundance in the coming decades.

4.1. Atlantic

The Canary Islands and associated island archipelagos (Madeira, Selvagens, Açores, Cabo Verde) that comprise Macaronesia form a distinct biogeographic region of volcanic origin, relatively isolated, and characterized by high endemism and biodiversity (Friedlander et al., 2017). The increased incidences of CFP in the last decade (Pérez-Arellano et al., 2005; Boada et al., 2010; Otero et al., 2010; Bravo et al., 2015) are understandable considering the discovery of two new *Gambierdiscus* species (*G. excentricus* and *G. silvae*) both of which are toxic (Fraga et al., 2011; Fraga and Rodríguez, 2014; Rodríguez et al., 2017; Robertson et al., 2018; Table 1). A high-density bloom of *G. caribaeus* in the Canary Islands reported by Soler-Onís et al. (2016) suggested the potential for toxic blooms and increased CFP incidences caused by eating local, toxic fish (Pérez-Arellano et al., 2005; Litaker et al., 2017).

The distribution of the five *Gambierdiscus* species found in the Canary Islands provides important information on how these species may respond to climate change. The temperature regime throughout the Archipelago is subtropical with little seasonal variation (21–26 °C), yet *Gambierdiscus* species are not uniformly distributed across the Archipelago (500 km) (Rodríguez et al., 2017). The northern sides of these islands are more humid due to exposure to prevailing trade winds and more exposed to wind driven wave action and currents. The two eastern most islands and associated islets, formed before the western islands, are semi-arid and characterized by a smoother relief and less influenced by trade winds (Rodríguez et al., 2017). Not surprisingly, the two eastern islands of the Canary Archipelago, with less run off, and less wave action, have the highest abundance of *Gambierdiscus*. In contrast, the western islands, which receive more direct land runoff, and experience higher wave action from trade winds, support lower *Gambierdiscus* population densities.

The average water temperatures in Macaronesia are currently in the ~22 °C range. These temperatures are low enough so the projected 0.8 °C increase by 2055 (Fig. 1A, B) will likely foster increased growth of *G. excentricus* and *G. silvae* resulting in elevated CFP risk. Fish that feed predominantly in embayments or other low turbulence environments with reduced land runoff along the leeward side of the eastern islands would be expected to present the greatest risk.

4.2. Caribbean and Gulf of Mexico

In the Caribbean Sea projections of the mean decadal rate of warming indicate an acceleration of temperature increases of ~0.13 °C from 2000 to 2029, to 0.31 °C in the period 2030–2059, reaching about 0.41 °C during the years 2070–2099 (IPCC, 2007). Unlike other regions, the Caribbean Sea is expected to have a reduced seasonality. From 1985–2010 the average annual temperature range was 3.3 °C and is projected to decrease to 2.9 °C in the 2030s and to 2.3 °C in the 2090s.

Kibler et al. (2015) used temperature data from six sites from the Gulf of Mexico and the Caribbean Sea to inform an ensemble of eleven global climate models from the World Climate Research Programme Coupled Model Intercomparison Project Phase5 (CMIP5). Kibler et al. (2015) developed projections of water temperatures through 2099 and combined those with experimentally derived temperature vs. growth relationships for multiple strains of five *Gambierdiscus* and *Fukuyoa* species (Kibler et al., 2012) to examine how growth rates might change through the end of the twenty-first century. Model results suggest *G. caribaeus*, *G. belizeanus* and *F. ruetzleri*, all low toxicity species, could become increasingly dominant in the Caribbean (see Fig. 6 in Kibler et al., 2015). Lower temperature-adapted species like *G. carolinianus*, will likely become less prevalent due to temperatures exceeding their thermal tolerance limits as the Caribbean becomes warmer and more stable. The results also show as temperatures reach 31 °C the abundance of all *Gambierdiscus* and *Fukuyoa* species will decline to varying degrees, lowering surface population densities. These conditions will likely cause population shifts to lower depths where water temperatures may

be 0.5–1 °C cooler and light is still sufficiently high for robust growth ($> 40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Kibler et al., 2015). Cooler growth adapted species (possibly including highly toxic *G. excentricus* and *G. silvae*) are expected to undergo range expansion in the northern Gulf of Mexico and up the US Atlantic seaboard.

The Flower Garden National Marine Sanctuary in the northern Gulf of Mexico provides an example of how thermal tolerances can influence the range of *Gambierdiscus* species (Tester et al., 2013). The East and West Flower Garden Banks, located ~190 km off the coast of Texas between the 100 m and 200 m isobaths, harbored six of the nine *Gambierdiscus* and *Fukuyoa* species known to occur in the greater Caribbean Region with many sampling sites yielding three species per sample (Tester et al., 2013). The average temperatures at East and West Flower Garden Banks were 24.9 ± 3.5 °C (range 17.4–30.9 °C) and 24.8 ± 3.6 °C (range 17.6–30.6 °C) respectively. In contrast, Stetson Bank located 50 km northwest of the East and West Banks, between the 50 m and 100 m isobaths had annual average temperatures of 24.0 ± 4.2 °C (range 14.5–30.5 °C). Only one species of *Gambierdiscus*, *G. carolinianus*, was found there. Nearer to shore, in shallower water, Stetson Bank experienced winter temperatures below 15 °C, a temperature that only *G. carolinianus* could survive (Tester et al., 2013). This is an example of lower thermal tolerance exhibited by all tropical BHAB species that sharply defines where growth ceases and mortality occurs (Kibler et al., 2012; Xu et al., 2016). The species-specific UTL will be the primary factor in restricting the northern and southern most ranges of BHABS.

Since *Gambierdiscus* may proliferate in disturbed coral environments another significant concern, in the Caribbean, is the projected northward shift of the 28 °C isotherm, identifying areas of risk for coral bleaching. A 1–2 °C increase in mean temperature above the reference period (2000–2009) predicted by midcentury is considered significant when regional SST increases of as little as 0.1 °C can trigger elevated coral bleaching intensity and geographic extent (McWilliams et al., 2005). Other habitat disruptions are probable as more intense tropical storm seasons are anticipated leading to potential increases in BHAB habitat (Angeles et al., 2007; Boucaud-Maitre et al., 2018). In the northern Gulf of Mexico, the presence of ~4000 active and abandoned drilling platforms (Villareal et al., 2007) with 8000–12,000 m² of surface area each (Bull, 1989) also provide habitat for BHAB species. These changes could also positively affect *Ostreopsis* expansion in the region (e.g. Boisnoir et al., 2019).

4.3. Mediterranean

Regional weather patterns are expected to change in the Mediterranean with a gradual warming of 3.5–7 °C by 2070–2099 (Dünkeloh and Jacobeit, 2003). Hot summer conditions, exceptional in the reference period (1961–1990), are predicted to become the norm by mid twenty-first century with annual precipitation expected to decrease in southern Europe and Turkey (Lelieveled et al., 2012). Specifically, strong negative rainfall trends are predicted from the Iberian Peninsula (Trigo and DaCamara, 2000) through Turkey while strong positive trends in precipitation are predicted for the southeastern Mediterranean region (Ben-Gai et al., 1998).

A review by Calvo et al. (2011) summarized recent trends in seawater parameters in the Mediterranean Sea, with a special focus on the northwest basin. The temporal data series from L'Estartit station on the Costa Brava dating to 1974, shows an increase at a rate of 0.30 °C decade⁻¹ between the surface and 50 m depth, and of 0.19 °C decade⁻¹ from 50 m to 80 m depth. This warming occurred in all seasons of the year but was most pronounced in summer and autumn. Concerning sea level, the data obtained at L'Estartit station since 1990 documented an increase of 3.9 cm decade⁻¹. Intermediate and deep waters also are experiencing an increase in salinity since the mid-twentieth century although future trends are difficult to predict using available models.

Gambierdiscus, was detected in Crete (north Aegean Sea,

Mediterranean Sea) in 2008 (Aligizaki and Nikolaidis, 2008; Holland et al., 2013) and more recently in the Balearic Islands (western Mediterranean) (Laza-Martínez et al., 2016; Tudó et al., 2018). To date no CFP cases have been reported in the Mediterranean Sea but these findings raise an alert. *Gambierdiscus* and *Ostreopsis* (see below; Açaç et al., 2016) populations are likely to increase at numerous locations throughout the basin and especially the North African coast where temperatures are already relatively high (Fig. 1A, B).

The concept of using globally available and regionally pertinent meteorological data to inform predictions of *Ostreopsis* cf. *ovata* abundance in the Mediterranean was tested using ten variables to train a Quantile Random Forest model, for a single BHAB species over a limited geographical area (Asnaghi et al., 2017). After validation, day of the year and SST were found to be the most important predictive factors followed by salinity and the number of days with temperatures higher than 24 °C. The model provides a flexible tool allowing coastal managers to generate warnings for swimmers and the aquaculture industry. The predicted higher temperatures and greater number of high temperature days should stimulate more intense *Ostreopsis* blooms in the future.

In addition to temperature increases, the continuing alterations of coastal habitats in the Mediterranean Sea and other high-density metropolitan areas will further promote *Ostreopsis* blooms and associated toxicity events (Granéli et al., 2011; Rhodes, 2011; David et al., 2012a; Fraga et al., 2012). Presently over 50 % of Mediterranean coastlines are dominated by concrete structures (EEA, 2000). In some regions the growth of cities, ports, and industries has caused more than 90 % of the coastline to be developed (Cencini, 1998). This growth includes extensive installations of concrete infrastructure to support transportation (ports), energy (pipelines, power stations, oil and gas rigs), recreation (marinas) and coastal safety (breakwaters). Extensive destruction of natural habitats occurred and has favored the expansion of *Ostreopsis* that colonize turf algal communities that grow well on hard surfaces. Additionally, eutrophication associated with increasing coastal populations may foster increased *Ostreopsis* blooms. Overall, anthropogenic pressures act synergistically to accelerate climate-induced changes in coastal ecosystems (Meroni et al., 2018).

4.4. Sea of Japan

High genetic diversity within the genus *Gambierdiscus* is reported from the coastal areas of Japan (Hokkaido 42 °N to Ishigaki Island 22 °N) with five species/phylogenotypes present including a newly described one, *G. scabrosus* (Nishimura et al., 2013, 2016). They are distributed according to temperature with *G. cf. yasumotoi* (now *Fukuyoa*) restricted to the subtropical areas and *G. australes* occurring from the subtropical (24–28 °N) to the temperate (31–37 °N) islands with a tendency to dominate in the subtropical region (Nishimura et al., 2013). Nishimura et al. (2013) reported the highest latitude location for *Gambierdiscus* and followed on with a five-year study (2007–2013) of seasonal population dynamics. *Gambierdiscus* cell abundance was positively correlated with SST, negatively correlated with salinity and no macroalgal substrate preferences were observed (Nishimura et al., 2018). The more toxic *Gambierdiscus* species were prevalent in subtropical islands and there is concern their habitat could expand northward with ocean warming. The presence of *Ostreopsis* cf. *siamensis* in the Sea of Japan at latitudes as high as 43°10' N (Selina et al., 2014), where temperatures range from 7 to 25 °C, suggests further potential northward expansion in this region as well. The implication is that climate driven temperature increases will foster greater BHAB population densities and associated toxin production over their current ranges. It also may elevate the risk in more highly populated regions where toxicity has not traditionally been an issue.

4.5. Central Pacific

One of the largest and most important cycles linking oceanic and atmospheric conditions is the El Niño/Southern Oscillation (ENSO), which originates in the tropical Pacific. Largely expressed in the tropical ocean as interannual changes in sea level and ocean temperatures, it is the "strongest natural interannual climate signal and has widespread effects on the global climate system and the ecology of the Tropical Pacific" (Latif and Keenlyside, 2009). ENSO responses will modify regional temperatures and precipitation patterns in ways that are expected to influence the growth potential of *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* species in both tropical and temperate latitudes as well (Hales et al., 2001; Gingold et al., 2014). Llewellyn (2010) used the South Pacific Epidemiological and Health Information Service (SPEHIS) dataset, the longest term and most robust CFP data set available and found statistically significant correlations between CFP incidences and the ENSO Index. His goal was to reexamine the association between SST and CFP in the South Pacific. This study defines two thresholds. First, temperatures must be warm enough for a long enough period to lead to CFP. The second threshold is when SSTs are above 30–31 °C for extended periods leading to a decline in CFP incidences. Presumably, prolonged temperatures > 30 °C exceed the thermal tolerance limits and cause a decline in *Gambierdiscus* abundance, thereby accounting for the reduction in CFP at these higher temperatures (Llewellyn, 2010).

Research efforts by the Institut Louis Malaré in Papeete (Tahiti, French Polynesia) and their international collaborations (Chinain et al., 1999a, 1999b; 2010; Morin et al., 2016; Darius et al., 2017, 2018a, 2018b) serve as a nexus for molecular identification, analytical techniques and innovate epidemiology reporting focused on assessing *Gambierdiscus* distribution and abundance and determining human health risk. A state-of-the-art example of the important role of how species composition influence toxicity follows.

Nuka Hiva Island in the Marquesas Archipelago in French Polynesia shares a robust assemblage of *Gambierdiscus*, similar to those found in the Canary Islands, and many locations in the Caribbean (Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB), 2012; Tester et al., 2013; Darius et al., 2017). After both sea urchin and gastropod poisoning outbreaks in Nuka Hiva in 2014, sampling of *Gambierdiscus* species, cell abundances and toxicity of the lower food web was instituted in three similar bays. Darius et al. (2017) provided clear evidence that the highest toxicity occurred in the bay where the most toxic *Gambierdiscus* species, *G. polynesiensis*, dominated indicating that local *Gambierdiscus* species assemblages are key to understanding toxicity and risk to human health. We know species matter, but we do not yet understand all the complex interactions that favor one species over another in similar habitats. While making general predictions about how climate change will affect species abundance and toxicity at regional levels, the complex interactions that determine relative species abundances that modulate CFP risks in local environments are not well-understood (Wells et al., this issue)

4.6. Western Pacific and Indian Oceans

The western Pacific Ocean has a vast number of islands and island archipelagos and many have not been sampled for BHAB species. Regional seas adjacent to the Malaysian peninsula south to Sumatra, to Java, across to Papua New Guinea and then north along the Philippine Trench to the South China Sea hold great potential for discovery of new species as was illustrated by the recent description of *G. balechii* from the Celebes Sea (Fraga et al., 2016). Of any region, sampling this one is the most challenging because of the vast distances and logistical adversities. There are, however, active research groups in Malaysia where *G. belizeanus* was identified on Malaysian Borneo and innovative microhabitat work is in progress with both *Gambierdiscus* and *Ostreopsis* (Leaw et al., 2011; Tan et al., 2013; Bloh et al., 2016; Yong et al., 2018). Across the basin in the Philippines *Gambierdiscus* has been detected and

CFP recognized in the region, although it is not common (Mendoza et al., 2013; Pocsidio and Dimaano, 2004; Vacarizas et al., 2018). Current data show predicted changes in temperature and salinity may slightly increase toxicity risk in some areas but cause a decline in toxicity over most of the warm pool region as temperatures exceed species-specific UTL of 30–31 °C for significant portions of the year.

This, too, is the situation for much of the Indian Ocean, except for outposts in Mayotte and Réunion Islands. Long-term datasets (Grzebyk et al., 1994; Thomassin et al., 1992; Turquet et al., 2001) and robust documentation of the evolution of *Gambierdiscus* populations after incidences of coral bleaching are available for Mayotte Island. In Réunion Island the epidemiology of CFP between 1986–1994 was well correlated with *Gambierdiscus* abundance (Turquet et al., 2001). These islands are among those surrounding Madagascar where in 1993, a mass poisoning hospitalized 188 victims, all of whom ate meat from a single shark (Diogène et al., 2017). It was from this shark that an Indian Ocean ciguatoxin was isolated and characterized (Hamilton et al., 2002). Waters adjacent to many of the islands in the western Pacific and Indian Oceans, if they do not warm beyond the thermal tolerances of *Gambierdiscus*, may provide the most extensive habitats for increased growth by 2055.

4.7. Australia, New Zealand and Tasmania

El Niño/Southern Oscillation (ENSO), in Australia is largely expressed as interannual changes in sea level and ocean temperatures but also affects major boundary currents. There is evidence of the strengthening of the East Australia Current, the dominant western boundary current, transporting tropical waters southward from the Great Barrier Reef (Queensland) to New South Wales and increasing water temperatures 0.75 °C (Ridgeway and Hill, 2012; Xu et al., 2012; Farrell et al., 2017). Coincidentally, most cases of CFP in Australia are reported from the tropical state of Queensland adjacent to the Great Barrier Reef (Lehane and Lewis, 2000), the site of a new species, *Gambierdiscus lapillus* (Kretzschmar et al., 2017). Prior to 2014, CFP was rare south of Queensland, but since then nine incidents affecting thirty-seven individuals have been reported (Farrell et al., 2016b). Range extensions of *Gambierdiscus* from the Great Barrier Reef southward have been suggested by both Farrell et al. (2017) and Sparrow et al. (2017) who venture that changes in distribution and abundance of migratory fish species and *Gambierdiscus* are both due to global warming. The predicted temperature changes are likely to support more extensive expansion of CFP risk south of Queensland and along the western coast (Fig. 1A, B). With no toxic *Gambierdiscus* species recorded in Australian waters yet (Larsson et al., 2018a), subtropical Australia is suggested as a sentinel location for monitoring range extensions of toxic species.

In New Zealand water temperatures are predicted to warm by 0.8–1.4 °C by 2055 with increases in sea level of 0.1–0.3 m (Fig. 1A, B; Lundquist et al., 2011). Significant precipitation changes are predicted with increases in the west, reduced rainfall in the east and more intense events. Runoff, changing inundation patterns and increased vulnerability to storm surge all have consequences for coastal ecosystems. Like the islands of Macaronesia in the Atlantic Ocean or Stetson Bank in the northern Gulf of Mexico, northern New Zealand could serve as a sentinel site for the expansion of *Gambierdiscus* and *Fukuyoa* species in the region (35°15'S). *Gambierdiscus* cf. *yasumotoi* (now *Fukuyoa yasumotoi*) (Rhodes et al., 2014) was recorded in New Zealand (Bay of Islands) during late austral summer sampling (Rhodes et al., 2014). Subsequently, Smith et al. (2017) recorded *F. paulensis* from Northland, New Zealand. The anticipated temperatures over the next century are expected to become more favorable for a variety of *Gambierdiscus* species as well. In this context, it is important to note the location of New Zealand relative to the North Meyer and Kermadec Island (28 °S) and the Cook Islands (21 °S), where two new *Gambierdiscus* species were recently discovered: *G. honu* (Rhodes et al., 2017a), and *G. cheloniae* from Rarotonga (Cook Islands) (Smith et al., 2016). Twelve of the

fifteen described species of *Gambierdiscus* occur on these and other island archipelagos in the region (Rhodes et al., 2017b). The North Meyer and Kermadec Islands, the Cook Islands and many others are influenced by the South Pacific gyre circulation which flows across the central Pacific and then southward toward New Zealand. This current system may allow *Gambierdiscus* rafting on materials such as seaweed to colonize New Zealand (Faust and Tester, 2004; Larsson et al., 2018b). Rhodes et al. (2017a,b) suggests another potential mechanism that allows transport of *Gambierdiscus* among island archipelagos via rafting pumice following submerged volcanic activity. These data are consistent with introductions of *Gambierdiscus* species into New Zealand, where they may find suitable habitat in the future increasing long-term toxicity risk.

The moderate climate of New Zealand and Tasmania has already provided good habitat for *Ostreopsis*. Surveys conducted from 1995 to 1997 on the northern most shores of the North Island of New Zealand recorded three species of *Ostreopsis* (*O. siamensis*, *O. lenticularis* and *O. ovata*) south of 35°S latitude (Rhodes et al., 2000; Chang et al., 2010). Chang et al. (2010) describe all three species were widespread and had substantially higher cell abundances in austral summer. In the summer of 2004, an unprecedented bloom of *O. siamensis* covered 30–60 % of the protected reef areas and caused disruptions to the lower trophic food web (Shears and Ross, 2009). The distribution of *Ostreopsis* species in Australia is not as well documented. Verma et al. (2016a), reported *Ostreopsis* from north Queensland (18°S) to Tasmania (41–43°S) from temperate shellfish growing estuaries around New South Wales (Ajani et al., 2013) with persistent occurrences in Merimbula Lake inlet throughout the year. Pearce et al. (2001) recorded *O. siamensis* blooms, but only in summer, in temperate lagoons along the Tasmania east coast (41–43°S) and noted their preference for high salinity, low turbidity and low nutrient conditions. Cumulatively, these data predict *Ostreopsis* range extensions and increased population densities over the course of the century as temperatures in this region increase by 0.6–1.2 °C (Table 2).

5. Summary

The purpose of a review of any area of research is to determine what is known and what we have yet to learn. With climate change oceans are predicted to warm by 0.4–1.4 °C mid-century and we expect the ranges of *Gambierdiscus*, *Fukuyoa* and *Ostreopsis* to expand beyond their traditional latitudes with cooler adapted species leading the colonization process. The warmer temperatures will also foster higher growth potential in many regions and is expected to increase overall cell abundances. The major exceptions are equatorial regions, where SSTs regularly exceed upper thermal limits (30–31 °C) causing a loss of habitat. In these instances, species may retreat deeper in the water column. The degree of range extension will further depend on species-specific habitat requirements and changes in regional meteorological conditions. The living substrates upon which BHABs depend (macrophytes, algal turfs and corals) as well as other biotic interaction also will be altered in complex ways that effect the extent and location of range extensions.

Our ability to predict how climate change will affect toxicity is limited for several reasons. Chief among these is the lack of key physiological and / or toxicity data. For *Gambierdiscus* and *Fukuyoa* species, it is hypothesized that relatively few species (*G. excentricus*, *G. polynesiensis*, *G. silvae*, *G. scabrosus* and possibly *G. australes*) produce sufficient toxicity to cause ciguatera fish poisoning. Growth vs temperature data are currently unavailable for *G. excentricus* and *G. polynesiensis*, two of the most toxic species. This paucity of critical species-specific information precludes our ability to predict climate driven changes in toxicity. For *G. australes*, where temperature versus growth and toxicity data exist, the situation is complicated by apparent regional differences in toxicity. Reports of high toxicity are known from some regions while in others toxicity seems to be absent. Until these

geographic toxicity patterns are confirmed, predictions regarding climate driven changes in toxicity risk are premature. Additionally, toxicity and physiological data are generally lacking for newly described species. This limits our ability to know how climate change will affect toxicity beyond the simple hypothesis that toxicity risk will increase as the growth of toxic species increases with higher temperatures, lower pH and higher CO₂ levels. Acquiring the growth and toxicity data for all species producing ciguatoxin-like compounds should be a priority for future research.

Another challenge is understanding how microhabitat structures select for some *Gambierdiscus* and *Fukuyoa* species and not others (Tan et al., 2013; Yong et al., 2018). Why some areas harbor highly toxic species while other, ostensibly similar habitats, do not is critical for identifying localized “ciguatera hot spots” with high numbers of ciguatoxic fish (Darius et al., 2018a,b; Hardison et al., 2018; Loeffler et al., 2018).

Predicating toxicity in *Ostreopsis* species is even more complicated because species identifications are not generally well resolved and standards of putative palytoxin and analogues are lacking, so assessment of toxicity has been difficult. While *O. cf. ovata* is likely the most toxic species, the link with aerosolized toxins has not been demonstrated yet and needs clarification. Current studies suggest that *Ostreopsis* risk to human populations in the Mediterranean is manageable. This may not be the situation in tropical regions where dramatic health impacts related to the highly toxic *Ostreopsis* species were reported (Deeds and Schwartz, 2010). Studies aimed at obtaining physiological and toxicological data from genetically identified isolates of the various BHAB species are critically needed. Without basic biological parameters to pair with environmental data, opportunities to benefit from increasingly sophisticated modeling efforts to examine the effects of climate change on distribution, abundance and toxicity of BHABs will be lost (Kibler et al., 2017).

“CFP stands at the international crossroads of epidemiology, ecology, technology, culture, and commerce” (Friedman et al., 2017). As we overlay the complicating factors associated with climate change, documenting the shifts in biogeographic domains occupied by BHAB species in the future and quantifying the risks they pose requires strategic and continuous monitoring focused on sentinel sites. It is reasonable to incorporate new technologies for toxin detection into monitoring protocols (Dechraoui Bottein and Clausen, 2017; Murray et al., 2018) but the predictive abilities to manage human health risk comes from first-tier field information provided through monitoring programs. These efforts detect environmental conditions that are conducive to high biomass events and allow time for planning and intensified sampling before toxins accumulate in marine food webs. Monitoring programs need to be strategically located and continuously maintained. Most importantly, monitoring samples need to be identified to species because of the variability in toxin content among species and the human health risks associated with greater cell abundances or geographic expansion of BHABs (Chinain et al., 2010; Litaker et al., 2017; Pisapia et al., 2017).

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